

Homoplastic Loss of Dart Apparatus, Phylogeny of the Genera, and a Phylogenetic Taxonomy of the Helminthoglyptidae (Gastropoda: Pulmonata)

by

BARRY ROTH

Museum of Paleontology, University of California, Berkeley, California 94720, USA

Abstract. The pulmonate land snail clade Helminthoglyptidae is redefined as *Helminthoglypta tudiculata* (A. Binney, 1843) and all gastropods that share a more recent common ancestor with it than with the clade (Xanthonychidae, Bradybaenidae)—the first phylogeny-based, rather than character-based, definition of this taxon. Many prior definitions of the group included a geographic component. Maximum-parsimony cladistic analysis was performed on 22 terminal taxa (named and unnamed) conventionally referred to the Helminthoglyptidae. The data set includes 21 multi-state shell, integument, and reproductive system characters. The resulting phylogenetic hypothesis indicates that absence of a dart sac is a homoplasy, originating at least six times; total absence of mucus glands originated homoplastically at least five times. The taxa usually assigned to *Sonorella* form a basal clade (SONORELLAMORPHA) that is the sister group of the rest of the Helminthoglyptidae (HELMINTHOGLYPTAMORPHA). Because SONORELLAMORPHA and HELMINTHOGLYPTAMORPHA share no common ancestor not also shared by the presumptive sister group (Xanthonychidae, Bradybaenidae), the monophyly of Helminthoglyptidae of authors is open to question. More information is needed to determine whether SONORELLAMORPHA is contained within HELMINTHOGLYPTIDAE as defined herein. The results of the analysis are expressed in a rank-free, phylogeny-based taxonomy. Four new genus-group taxa and 11 suprageneric taxa are described.

INTRODUCTION

The pulmonate land snail taxa of western and southwestern North America belonging to the Helminthoglyptidae are numerically significant—46% of the species of native land mollusks in California (Roth, unpublished); 45% of the species in Arizona (Bequaert & Miller, 1973)—and potentially important for understanding regional climatic history and biogeography (Smith et al., 1990). Patterns of ancestry and descent among these taxa usually have been addressed only on a case-by-case basis, and published classifications have not had a phylogenetic underpinning. A rigorous phylogenetic hypothesis is needed for meaningful further study.

Supraspecific taxonomy of the group has been based largely on accessory reproductive structures, including mucus glands and dart sac, which function in courtship and mating (Webb, 1942, 1951, 1952a). Absence of these structures in many genera is widely thought to be due to secondary simplification, although this assumption remains

basically untested. A lively debate exists as to how many times the loss of dart sac and/or mucus glands has occurred.

The purpose of this paper is to apply the methods of phylogenetic systematics (Hennig, 1966; see also Wiley, 1981; Brooks & McLennan, 1991) to the analysis of evolutionary relationships among the genera contained in Helminthoglyptidae as defined herein. I used the program HENNIG86 (Farris, 1988) to generate a set of maximum-parsimony cladograms based on 22 terminal taxa and 21 characters representing 61 character states; a strict consensus tree (Nelson, 1979) is presented to show the groups in common to the resulting cladograms and used as a basis for discussion of the taxonomy of the Helminthoglyptidae.

The cladograms allow an estimate of the extent of homoplasy represented by absence of dart sac and mucus glands, and also, for each case, whether that absence is apomorphic or plesiomorphic with respect to its ingroup. Absence of dart sac and absence of mucus glands were not included in the originally analyzed data set, but were mapped afterward on the consensus tree.

Historically, Helminthoglyptidae has undergone several definitions and redefinitions. Dart-bearing helicoids of the Americas were long included in a broadly construed family Helicidae Rafinesque, 1815, roughly equivalent to what conventional land snail taxonomy now designates as the suborder Holopoda. Pilsbry's (1893–1895) “Belogona Euadenia” contained taxa with “mucus glands sacculated, club-shaped, bulbous or flattened, glandular, inserted on dart sack or at its base . . .” (Pilsbry, 1893–1895:xxxvi), spread among 12 genera. The primary division of Belogona Euadenia was into American and Eurasian groups, without supporting characters (Pilsbry, 1893–1895:xxx). The taxa considered in the present paper were included in the “sections” *Micrarionta* Ancy, 1880, and *Helminthoglypta* Ancy, 1887, of genus *Epiphragmophora* Döring, 1875.

Pilsbry (1939:1, 24) named the family Helminthoglyptidae, typologically defined by the genus *Helminthoglypta* (type species *Helix tudiculata* A. Binney, 1843). His diagnosis, “dart sac or sacs and mucous glands present, the latter club-shaped, globular or irregular (not tubular or finger-shaped), inserted close to the base of the dart sac; talon short, concealed in the albumen gland; shell usually with a band above periphery, or sometimes with three or many bands, the lip from simple to reflected, not toothed” (Pilsbry, 1939:1), differentiated Helminthoglyptidae from Camaenidae, Sagdidae, and Polygyridae (“no dart apparatus, talon exposed”) and from the remainder of the old Belogona (in which the mucus glands are tubular or fingerlike). He also provided an enumerative definition—that is, he pointed to the taxa he expected to conform to his character-based definition—stating that the family included “the American dart-bearing helices” (Pilsbry, 1939:25).

Pilsbry (1939) also named the subfamily Sonorellinae (originally including only the genus *Sonorella* Pilsbry, 1900, but later amended [Pilsbry, 1948:1093] to include *Sonorelix* Berry, 1943) for species lacking the diagnostic dart sac and mucus glands but agreeing with the rest of the Helminthoglyptidae in shell, jaw, and talon characters. In an insight with lasting impact on helminthoglyptid taxonomy, he inferred that the reproductive system in Sonorellinae is secondarily simplified,¹ but he did not provide a test of whether the dartless condition is apomorphic or plesiomorphic.

For nearly 40 years Pilsbry's concept of Helminthoglyptidae was widely accepted and the taxa defined by its enumerative/geographic and character-based definitions

assumed to be coextensive. Baker (1956, 1959) observed that the earliest family-group name based on a member of the group was Xanthonychidae Strebel & Pfeffer, 1879 (based on *Xanthonyx* Crosse & Fischer, 1867), and a minority of authors adopted Xanthonychidae as the name to use, but the family's diagnosis and scope went largely unchallenged. Richardson (1982) catalogued the species.

Schileyko (1978, 1979) removed the Humboldtianinae, in which multiple dart sacs subtend compact mucus glands surrounding the vagina, from Helminthoglyptidae. Miller (1987), Miller & Naranjo-García (1991), and Evanoff & Roth (1992) followed Schileyko in recognizing Humboldtianidae as a distinct taxon.

Nordsieck (1987; translation by Emberton, 1992) revised the systematics of the Helicoidea at the family level, using cladistic methods to derive a statement of relationships among Xanthonychidae, Sphincterochilidae Zilch, 1960, Hygromiidae Tryon, 1866, Helicidae, and Bradybaenidae Pilsbry, 1934. His classification below the level of family was not based on the principle of grouping by synapomorphy, but relied on arbitrary magnitude of difference and gradal criteria (e.g., his refusal [Nordsieck, 1987:19] to group shelled snails and semislugs in a single subfamily). It included numerous new subfamilies and tribes, many of them monotypic at the next lower category (e.g., Monadeniinae, new subfamily for genus *Monadenia* Pilsbry, 1895; Bunnyini, new tribe for *Bunnya* Baker, 1942) and apparently proposed as much for “bookkeeping” reasons as for their information content (cf. Simpson's [1961] advocacy of exhaustive subsidiary taxa, and critique of same by Farris [1976]). His taxon definitions were partly character-based and partly enumerative. The character-based component was not rigorously diagnostic (for Helminthoglyptini, “diverticulum present; stimulatory organ present, lacking in one group”; for Sonorellini, “diverticulum usually lacking; stimulatory organ lacking” [Nordsieck, 1987:20; Emberton translation]); the enumerative component was rather casually employed, as in references to the otherwise undefined “*Micrarionta*-Gruppe” and “*Sonorella*-Gruppe,” and sometimes erroneous (*Micrarionta*, placed by Nordsieck in the Helminthoglyptini, lacks a spermathecal diverticulum).

Miller & Naranjo-García (1991) used magnitude of difference criteria to modify the cladistic family-level classification of Nordsieck (1987). They redefined Helminthoglyptidae as helicoid snails having, in dart-bearing species, one or both mucus glands consisting of wide membranes that wrap around parts of the anterior end of the reproductive tract. Under this definition, Helminthoglyptidae consists of a number of genera of the North American west and southwest, distinguished from Mesoamerican genera (Xanthonychidae) in which mucus glands are nodulose, tubular, or vesicular. They reassigned *Monadenia*, formerly considered a genus of Helminthoglyptidae, to Bradybaenidae. Like Pilsbry (1939), Miller & Naranjo-García (1991) included genera that lack mucus glands and dart apparatus through secondary simplification but did

¹ It was not the first time he had done such a thing. In Pilsbry & Vanatta (1898:68), he referred to the absence of mucus glands in *Glyptostoma* Bland and Binney, 1873, as “a degenerative feature unique in *Belogona Euadenia*.” *Glyptostoma* is now assigned to the Megomphicidae. The possibility of a cultural predisposition to see taxa lacking certain organs as derived or degenerate belongs properly to the history of science; I will not pursue it further here, except to note that Roth (1981) remarked on a parallel case in the early taxonomy of *Monadenia*.

not specify other morphologic criteria for inclusion of these genera. They stated that loss of mucus glands and dart apparatus had happened multiple times (citing Miller, 1970, 1973, 1981a), so that Sonorellinae of Pilsbry and Sonorellini of Nordsieck were polyphyletic groups.²

Schileyko (1991) proposed a systematic revision of the Helicoidea *sensu lato* based entirely on the characters of the lower part of the reproductive tract. He hypothesized an archetypal, ancestral form and from there spun an imaginative evolutionary history for the superfamily. The narrative consists of a series of sketches explaining how certain configurations of the genitalia could have come about through changes to other (mostly existing) configurations; hypothetical configurations were introduced as necessary. Criteria of parsimony or independent characters supporting or falsifying these hypotheses of ancestry and descent were not considered.

Schileyko's (1991) innovations in classification included Eremariontinae, a new monotypic subfamily of Helminthoglyptidae, for *Eremarionta* Pilsbry, 1913; removal of all dartless genera from Miller & Naranjo-García's (1991) Helminthoglyptidae to subfamily Sonorellinae of Xanthonychidae; and new subfamily Micrariontinae of Xanthonychidae. A character-based and an enumerative definition were provided for each family-group taxon, but the arrangement of taxa was based largely upon the evolutionary narrative and gradal criteria. Because many genera were considered to be derived directly from other genera (e.g., Schileyko, 1991:fig. 7), the system included numerous paraphyletic groups.³

Emberton (1991) cladistically analyzed 17 family-group taxa of land snails, including Helminthoglyptidae, in a search for the closest outgroup of Polygyridae. *Helminthoglypta tudiculata* represented Helminthoglyptidae in the analysis; *Cepolis varians* (Menke, 1829) represented Xanthonychidae. Maximum-parsimony analysis generated a consensus tree containing the polytomy (Helminthoglyptidae, Xanthonychidae, Bradybaenidae, Polygyridae, (Thysanophoridae, (Camaenidae, Sagdidae))). This clade is united by the synapomorphies of descending ureter partly or variably roofed, ureteric interramus shallowly and broadly excavated, and left parietal and visceral ganglia fused.

² This is not quite fair to Nordsieck, who had stated that groups resulting from parallel evolution ought not to be united in the single subfamily Sonorellinae and, citing Miller as authority, that there were additional groups without a dart sac, independent of the "Sonorella-Gruppe" that made up his Sonorellini (Nordsieck, 1987:19, 20). He placed the dartless genus *Greggelix* in Helminthoglyptini.

³ Solem (1991) criticized the Schileyko classification as "mal-acological hyperinflation" because certain groups of taxa were recognized at higher categoric levels than was traditional. This comes down to an argument about taste in ranking: Solem did not maintain that the groups recognized by Schileyko were anything other than natural, monophyletic groups or propose any alternative set of relationships among them.

The distinction between Xanthonychidae as restricted by Miller & Naranjo-García (1991) and Bradybaenidae needs further investigation. Schileyko (1991) reassigned *Monadenia* (as subfamily Monadeniinae) to Xanthonychidae, but it is pointless to argue the allocation until an objective morphological distinction between Xanthonychidae and Bradybaenidae is in place. In common with the Asian Bradybaenidae (Azuma, 1982) and apparently with Central American Xanthonychidae (e.g., *Trichodiscina* Martens, 1892), *Monadenia* has a fundamentally four-banded shell (Roth, in preparation). In the few multiple-banded helminthoglyptids (some species of *Xerarionta* Pilsbry, 1913), the banding is complex and not obviously four-fold. The lower, ductlike portion of the mucus gland in *Monadenia* may be homologous to the Nebensack in other Bradybaenidae (A. A. Schileyko, written communication, 1990). Xanthonychidae and Bradybaenidae both have a single dart sac, homoplastic with the single dart sac in Helicidae, according to Schileyko's (1991) narrative, but possibly homologous with that in Helminthoglyptidae.

I provisionally regard (Xanthonychidae, Bradybaenidae) as the sister group of Helminthoglyptidae. Other groups, such as Helicostylidae Ihering, 1909, and Epi-phragmophoridae Hoffman, 1928, are too poorly known to be considered at this time.

In recent years, it has become increasingly clear that conventional biological taxonomy (that is, the taxonomy of which the nomenclatural expression is the subject of the International Code of Zoological Nomenclature) is limited in its ability to express the evolutionary relations that are the concern of phylogenetic systematics. One radical solution, taxon definitions based on phylogenetic relationships, has been explored in several recent papers (Wiley, 1979, 1989; Rowe, 1987; de Queiroz, 1988; Gauthier, Estes & de Queiroz, 1988; de Queiroz & Gauthier, 1990, 1992). In this paper I propose a taxonomy of the Helminthoglyptidae (I deliberately avoid the term "classification" for reasons discussed by de Queiroz & Gauthier, 1990) that is based on the phylogenetic hypothesis generated by this study. Between the most inclusive taxon (Helminthoglyptidae) and the least inclusive (species), the system conflicts in many ways with the traditional ("Linnaean") classification. Because the taxa of the phylogenetic taxonomy are all monophyletic groups by definition, I believe this system will prove more useful for future analysis than the traditional classification.

For purposes of this study, I define Helminthoglyptidae as *Helminthoglypta tudiculata* (A. Binney, 1843) and all gastropods that share a more recent common ancestor with it than with the clade (Xanthonychidae, Bradybaenidae). This is the first phylogeny-based definition of the family; all previous definitions have been character-based. It is a stem-based definition (de Queiroz & Gauthier, 1990, 1992) (that is, one that specifies the meaning of a name by associating the name with a clade of all organisms sharing a more recent common ancestor with one designated descendant than with another).

Under the present state of knowledge, an apomorphy-based definition (de Queiroz & Gauthier, 1990, 1992) that takes in the same membership is “the first helicoid snail to have one or more membranous mucus glands, and all of its descendants.” Both definitions define monophyletic taxa (a monophyletic taxon [*sensu* Farris, 1974; = holophyletic, Ashlock, 1971] is composed of an ancestor and all of its descendants). Taxa could be discovered that are members of the stem-based taxon but not of the apomorphy-based taxon (Figure 1). Because at present both taxa seem to comprise the same array of subordinate taxa, I propose no separate name for the apomorphy-based taxon. This study can be viewed as a test of the hypothesis that Helminthoglyptidae of Miller & Naranjo-García (1991) and Helminthoglyptidae as defined herein are coextensive. As shown below, the inclusion of the taxa conventionally referred to *Sonorella* is problematical.

PREVIOUS WORK ON PHYLOGENY OF TAXA OF HELMINTHOGLYPTIDAE

Here follows a brief chronologic review of previous work touching on the phylogenetic relationships among taxa in the Helminthoglyptidae. Discussions in which “relationship” is equated with similarity or with membership in a particular character-based group, without explicit evolutionary implications (e.g., Berry, 1943, 1947) are omitted.

Webb (1952b) stated that the Sonorellinae evolved from *Micrarionta* by loss of dart and mucus gland systems.

Gregg (1960) briefly hypothesized reproductive system transformations: increased complexity in *Helminthoglypta* and loss of diverse structures in other genera.

The revisionary thesis of *Sonorella* by Miller (1967a) introduced the concept that the absence of dart sac and mucus glands was homoplastic, citing as examples (1) *Mohavelix micrometalles* (Berry, 1930) from the El Paso Mountains, eastern Kern County, California, formerly assigned to *Sonorella* but conchologically more similar to *Chamaerionta aquaealbae* (Berry, 1922) and thought to be derived from a common ancestor with it; and (2) populations of *Eremarionta argus* (Edson, 1912) from the Argus Mountains, Inyo County, California, that lacked any trace of dart sac and mucus glands. He invoked “saltational” chromosomal reorganization (Lewis, 1966), occurring in marginal, intensely interbreeding populations, for the seemingly drastic and sudden loss of reproductive structures.

Gregg & Miller (1969) described *Sonorella allynsmithi* from the Phoenix Mountains, Maricopa County, Arizona, noting that the habitat was more typical of *Eremarionta* than of *Sonorella* and that certain shell and anatomical characters were also *Eremarionta*-like. They stated that the similarity might be due to convergent evolution or might “tend to point to *S. allynsmithi* as a relatively unchanged descendant of the ancestral *Sonorella* founder” (Gregg & Miller, 1969:92).

Miller (1970) described *Helminthoglypta micrometal-*

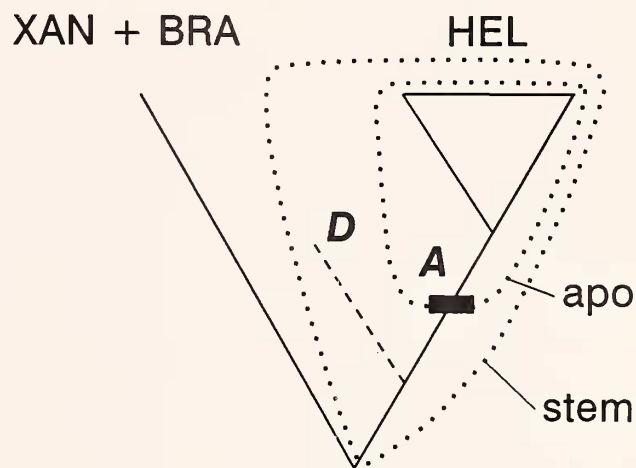


Figure 1

Relationship of apomorphy-based (apo) and stem-based (stem) definitions of HELMINTHOGLYPTIDAE (HEL). A = origin of autapomorphy; D = hypothetical newly discovered taxon; XAN+BRA = (Xanthonychidae, Bradybaenidae).

leoides from northern slopes of the El Paso Mountains, eastern Kern County, California, and suggested that it was ancestral to *Mohavelix micrometalles* from southern slopes of the same range. He mentioned six genera as (presumably independent) instances of secondary simplification of reproductive structures.

Miller (1971:64) stated that *Sonorella* “probably arose from a marginal population of *Sonorella* or *Eremarionta*.”

Miller (1972) proposed the new genus *Greggelix* for several species from Baja California, Mexico, and reaffirmed that evidence indicated that loss of dart apparatus had occurred more than once in Helminthoglyptidae.

Miller (1981a) proposed the new genus *Eremariontoides* for *Sonorella argus* Edson, 1912, of the Slate and Argus ranges, Inyo County, California, and suggested that it had “undergone major genetic changes from the populations in the Panamint and Avawatz ranges” (Miller, 1981a: 438–439) which he described as a new species, *Eremarionta greggi*.

Miller (1985:98) suggested that the new subgenus *Rothelix* “probably evolved from an *H[elminthoglypta]. traskii*-like ancestor and spread, during pluvial times, throughout the area that it now occupies.”

Pearce (1990) was the first author to apply explicitly cladistic methods to the analysis of relations among any helminthoglyptid genera. (*Monadenia*, cladistically analyzed by Roth [1981], is no longer considered helminthoglyptid; Nordsieck’s [1987] use of cladistic methodology was limited to taxa at the family level.) He presented (Pearce, 1990:figs. 5, 7) the tree (*Helminthoglypta*, ((*Plesarionta*, *Xerarionta*), (*Eremarionta*, *Micrarionta*))), with *Micrarionta* further analyzed into its component species. Pearce’s results have little applicability to the present study for several reasons: The group he analyzed was not hol-

ophyletic; only the above genera were considered, for the limited purpose of polarizing character-state transformations within *Micrarionta*. The data set (Pearce, 1990:table 3) includes erroneous anatomical information (e.g., absence of a spermathecal diverticulum in *Eremarionta*; presence of a verge in *Xerarionta* and absence of a verge in *Plesarionta*; presence of a dart sac in *Micrarionta opuntia*). The codings for presence/absence of papillae on embryonic whorls differ from my observations presented herein. The concepts of *Helminthoglypta* and *Eremarionta* are based on few species, resulting in an underestimated range of form—excluding, for example, *Helminthoglypta* species with closed umbilicus or depressed shell. The data set for the consensus tree (Pearce, 1990:fig. 7) is based predominantly on shell dimensions, doubtfully useful for broader intergeneric comparison. Five of the eight character-states that define node 4 of the consensus tree (that is, *Micrarionta*) are size-related characters that show reversals within the *Micrarionta* clade.

In his revision of the Helicoidea, commented on above, Schileyko (1991) reasserted monophyly of the Sonorellinae. He presented a scenario based solely on characters of the lower reproductive tract, in which genera were derived sequentially from other contemporary genera (*Mohavelix* Berry, 1943, from *Sonorella*; *Sonorella* from *Sonorelix*, and so forth). His “family trees” used cartoons emphasizing the characters that supported his scenario; other characters were selectively excluded from the discussion (e.g., the penial sheath of *Sonorella*). All genera, whether the monotypic *Eremariontoides* or the speciose *Sonorella*, were treated as single entities—grades—along a few linear evolutionary paths; there was no representation of the diversity of side branches. Schileyko’s (1991:223, fig. 5) depiction of *Eremarionta* and *Micrarionta* is incorrect in that mucus glands are shown inserting well up on the dart sac, remote from the vagina. In these genera the glands actually insert either on the vagina just above the opening of the dart sac or in the crotch between vagina and dart sac; the true condition is well illustrated by Pilsbry (1939) and Miller (1981a).

In summary, the present state of helminthoglyptid phylogenetics consists of two competing scenarios in which either one (according to Schileyko) or several (according to Miller) ancestral taxa with a “full kit” of accessory reproductive structures give rise to taxa lacking dart sac and/or mucus glands. Schileyko’s (1991) work is an excellent example of conjectural, narrative (*sensu* Ball, 1976) history: a series of “how-possibly explanations” (Dray, 1957; O’Hara, 1988). It is not couched in testable propositions and therefore provides no objective way of dealing with new data. It uses the four devices—graphical and textual sequencing of contemporary taxa, pruning of side branches, recognition of paraphyletic taxa, and differential resolution of different parts of the tree—criticized by O’Hara (1992) as harmful to representations of the evolutionary past.

The papers of Miller look mainly to present geographic neighbors for ancestry of dartless taxa (*Helminthoglypta*

micrometalleoides for *Mohavelix*; *Eremarionta greggi* for *Eremariontoides*; *Xerarionta* for *Greggelix*). This history is played out on a snail geography not very different to that of the present, and geological time, as far as it is considered, extends no farther back than “pluvial times” (Miller, 1985). Alternative theories of origin, and the extent to which other characters support or falsify them, are rarely considered. In this style of scenario-building, the fundamental assumption is of homoplasy—multiple origins of the dartless condition.

In contrast, the approach employed here starts with and maintains the assumption of homology until homoplasy is indicated by the weight of evidence from other, independent characters (Hennig, 1966; Brooks & McLennan, 1991). Since geography plays no part in the generation of the phylogenetic hypothesis, the hypothesis can be used to analyze biogeographic history of the group without introducing circularity into the argument. Similarly, excluding absence of dart sac and mucus glands from the data set analyzed and then mapping those absences on the consensus tree provides a non-circular approach to the number of independent origins of dartlessness.

MATERIALS AND METHODS

The terminal taxa entered in this analysis are listed alphabetically below, along with the representative species examined anatomically and references to published sources of information. I have examined shells of almost every species of the family, including at least one representative of every terminal taxon. Most reproductive system information is based on stained whole mounts prepared by the method of Miller (1967a). Emberton (1988) correctly pointed out limitations of the slide-mount method. I believe, in this instance, the ability to consult repeatedly numerous specimens permanently preserved in standard orientation justified reliance on whole mounts, as long as possible artifacts of the method were taken into account. Simultaneous dissection, recommended by Emberton (1991), was not possible in a situation where fresh material is unavailable for many scarce taxa.

The specimen lots consulted are too numerous for individual citation, but include material in my own reference collection, the Santa Barbara Museum of Natural History, the collection of Walter B. Miller, and the California Academy of Sciences.

Most of the terminal taxa originally were proposed as genera, subgenera, or informal groups (e.g., the *Sonorella hachitana* group of Pilsbry, 1939). Several nominal taxa were found to be diverse as to the characters analyzed and were divided into separate taxa (e.g., *Micrarionta*₁ and *Micrarionta*₂). In speciose terminal taxa of groups needing monographic revision (like *Charodotes*, where a verge is variably present or absent, or the subtaxa of *Sonorella*), separate taxa were considered early in the analysis, but were condensed into single taxa once it became clear that

Table 1

Distribution of character states among terminal taxa of Helminthoglyptidae and outgroup.

Terminal taxon	Symbol	Character no.			
		1-5	6-10	11-15	16-21
<i>Chamaearionta</i>	CHM	AABBA	EBDAB	ABCBB	BBCBAB
<i>Charodotes</i>	CHR	CBAAB	BBABB	AACAB	BBBBAB
<i>Coyote</i>	COY	CBAAB	BBABE	ACCAB	BBCBAB
<i>Eremarionta</i> ₁	ER1	AAABA	EBADB	ACCBB	BBBBBB
<i>Eremarionta</i> ₂	ER2	AAABA	BBACB	AACBB	BBBBBB
<i>Eremariontoides</i>	ERO	AE?BC	BBBDB	ACCBB	BBBBBB
<i>Greggelix</i>	GRE	ADBBC	CBCAB	AECAB	BBCBBA
<i>Helminthoglypta</i> ₁	HL1	CBAAB	BBABB	AACAB	BABBAB
<i>Helminthoglypta</i> ₂	HL2	ABAAA	BBABB	AACAB	BABBAB
<i>Herpeteros</i>	HER	AE?BC	EBDAA	ADCAB	BBBBBA
<i>Martirelix</i>	MAR	ADBBC	BBCAA	AFCAB	BBCBBA
<i>Micrarionta</i> ₁	MI1	AABBA	ABAAB	AECAB	BBBABB
<i>Micrarionta</i> ₂	MI2	ACBBC	ABAAB	AECAB	BBCABB
<i>Mohavelix</i>	MOH	AE?BC	ABBAB	AACCB	BBCBAB
<i>Myotophallus</i> ₁	MY1	AE?BC	ABBAA	ABFB	BBABAB
<i>Myotophallus</i> ₂	MY2	AE?BC	ABBAB	ABBBB	BBBBAA
<i>Plesarionta</i>	PLE	AABBA	CBCAB	AECDA	BAABAB
<i>Rothelix</i>	ROX	BBAAB	BBABB	BBCAB	BBBBAB
<i>Sonorelix</i>	SLX	AE?BC	DAAAB	AACCB	BBBBBB
<i>Sonorella binneyi</i> group	SNB	AE?BC	ABBAA	AAAFB	BBABAA
<i>Sonorella granulatisima</i> group	SNG	AE?BC	ABBAA	AGAGB	BBCBAA
<i>Sonorella hachitana</i> group	SNH	AE?BC	ABBAA	AGAFB	BBABAA
<i>Xerarionta</i>	XER	AABBA	CBCAB	ABCEA	AAABAB
outgroup	OUT	AABBA	ABAAB	AAABB	BBBBAB

they did not affect the framework of the cladograms being produced.

Analysis

Cladistic analysis of the taxon/character matrix (Table 1) was performed using the implicit enumeration algorithm of HENNIG86 (Farris, 1988) with the branch-breaking and successive approximations weighting procedures. From the set of minimum-length cladograms generated, a strict consensus tree (Nelson, 1979; Sokal & Rohlf, 1981) was computed. In the data matrix analyzed, character-state trees were represented by mixed coding (Brooks & McLennan, 1991). All character-states were treated as ordered. No weighting was assigned *a priori* to the characters of any one system; the successive approximations option of HENNIG86 reduced the number of equal-length cladograms by an iterative series of *a posteriori* weightings (Farris, 1969; Carpenter, 1988). Character-state transformations were polarized by outgroup comparison (Watrous & Wheeler, 1981; Brooks & McLennan, 1991). On the basis of Emberton's (1991) analysis of family-group taxa, (Xanthonychidae, Bradybaenidae) (represented by the genus *Monadenia*) was used as the outgroup for polarizing character-state transformations. Polygyridae was considered secondarily as an outgroup, with similar results.

Two aspects of land snail natural history influenced my

evaluation of hypothesized character-state trees based on outgroup comparison. In the past, there has been some tendency to regard the variety in helminthoglyptid reproductive structures as a non-adaptive consequence of genetic drift in small populations (e.g., Miller, 1967a:228-229); but explanations involving sexual selection seem just as worthy of consideration. As Leonard (1991:45) stated, "where genital anatomy is varied sufficiently to be a useful taxonomic character at the levels of genus, subgenus and species . . . sexual selection is likely to have been important." Sexual selection does not rule out (and Eberhard [1985] argued that it tends to produce) rapid evolutionary divergence in genital characters, which may appear "saltational" in hindsight, because it leaves few intermediates.

I also considered water conservation. Desiccation may be the main cause of snail death worldwide (Solem, 1984). The cost in moisture (through mucus secretion and evaporative loss) during prolonged courtship leads to the prediction that, in semi-arid and arid habitats, structural modifications and behavior that reduce water-loss during reproduction should be selectively favored. *Monadenia* and *Helminthoglypta* species from mesic habitats undergo prolonged courtship before mating (Webb, 1942, 1951, 1952a, b; author's observations). In the Arizonan *Sonorella simmonsii* Miller, 1966, which lacks dart sac and mucus glands, the snails merely approach one another and mate (Webb, 1990); I regard this as the derived condition. Solem &

Christensen (1984) reported extreme cases of camaenid snail matings lasting less than 10 minutes in seasonally arid parts of northwestern Australia.

Taxa Included and Data Sources

Chamaearionta Berry, 1930. Originally proposed as a subgenus of *Micrarionta*. Monotypic; type species *Micrarionta aquaealbae* Berry, 1922, examined. Anatomy described and illustrated: Pilsbry (1939), Gregg (1960).

Charodotes Pilsbry, 1939. Originally proposed as a subgenus of *Helminthoglypta*. Type species *Helix traskii* Newcomb, 1861. Species examined: *Helminthoglypta (Charodotes) traskii* and 13 of the 15 other recognized species (Roth & Hochberg, 1992). Anatomy described and illustrated: Pilsbry (1939), Webb (1952a), Miller (1981c), Roth (1973, 1987a), Roth & Hochberg (1992).

Coyote Reeder & Roth, 1988. Originally proposed as a subgenus of *Helminthoglypta*. Type species *Helminthoglypta (Coyote) taylori* Reeder & Roth, 1988. Species examined: *H. (C.) taylori* and the 11 other recognized Recent species (Reeder & Roth, 1988). Anatomy described and illustrated: Pilsbry (1939), Miller (1970), Roth & Hochberg (1988), Reeder & Roth (1988).

Eremarionta Pilsbry, 1913. Originally proposed as a "section" of *Micrarionta*; separated as a genus by Bequaert and Miller (1973). Type species *Micrarionta desertorum* Pilsbry and Ferriss, 1908. Species examined: *Eremarionta greggi* Miller, 1981; *E. indioensis indioensis* (Yates, 1890); *E. i. cathedralis* (Willett, 1930); *E. i. wolcottiana* (Bartsch, 1903); *E. mexicana* (Pilsbry & Lowe, 1934); *E. rowelli* (Newcomb, 1865), subsp. indet., from Mohawk Mountains and Little Harquahala Mountains, Yuma County, Arizona. Anatomy described and illustrated: Pilsbry (1918, 1939), Miller (1981a).

In *Eremarionta rowelli*, the spermathecal diverticulum is short (Pilsbry [1907, 1939] reported it absent in *E. r. hutsoni* (Clapp, 1907) and *E. r. desertorum* (Pilsbry & Ferriss, 1908); but according to Gregg [1960] and in all dissections I have examined, a short diverticulum is present) and the verge consists of a short, broad papilla. This taxon was entered as *Eremarionta*₁. In *E. greggi*, *E. indioensis*, and *E. mexicana*, the spermathecal diverticulum is of moderate length and the verge is roughly cylindrical or conic. These taxa were entered as *Eremarionta*₂.

Eremariontoides Miller, 1981. Monotypic; type species *Sonorella argus* Edson, 1912, examined. Anatomy described and illustrated by Miller (1981a).

Greggelix Miller, 1972. Type species *Helix indigena* Mabille, 1895. Species examined: *Greggelix indigena*; *G. loehrii* (Gabb, 1868); *G. punctata* Miller, 1981. Anatomy described and illustrated: Miller (1972, 1981b).

Helminthoglypta Ancy, 1887. Type species *Helix tudiculata* A. Binney, 1843. Species examined: *Helminthoglypta tudiculata* and 36 of the 40 other recognized species (Roth, unpublished data). Anatomy described and illus-

trated: Pilsbry (1939), Berry (1959), Gregg & Miller (1976), Miller (1985), Reeder (1986), Reeder & Miller (1986a, b), Roth (1987b, 1988a). This terminal taxon is equivalent to *Helminthoglypta*, *sensu stricto* of Roth & Hochberg (1992).

Most species of *Helminthoglypta* have an atrial sac; these were entered as *Helminthoglypta*₁. In *Helminthoglypta intersessa* Roth, 1987, the atrial sac is absent and the dart sac inserts directly on the vagina (W. B. Miller, personal communication, 1992); this taxon was entered as *Helminthoglypta*₂.

Herpeteros Berry, 1947. Originally proposed as a subgenus of *Sonorella*. Type species *Micrarionta (Eremarionta) inglesiana* Berry, 1928. Species examined: *Herpeteros inglesiana*, *H. peninsularis* (Pilsbry, 1916). Anatomy described and illustrated: Berry (1947), Gregg (1949), Miller (1972).

Martirelix Miller, 1982. Originally proposed as a subgenus of *Greggelix*. Type species *Greggelix (Martirelix) babrakzaii* Miller, 1982. Species examined: *G. (M.) babrakzaii*; *G. (M.) huertai* Miller & Roth, 1990. Anatomy described and illustrated: Miller (1982), Smith et al. (1990).

Micrarionta Ancy, 1880. Originally proposed as a subdivision of *Helix* Linnaeus, 1758; separated as a genus by Pilsbry (1913). Type species *Helix facta* Newcomb, 1864. Species examined: *Micrarionta facta*; *M. beatula* Cockerell, 1929; *M. feralis* (Hemphill, 1901); *M. gabbii* (Newcomb, 1864); *M. guadalupiana* (Pilsbry & Vanatta, 1898); *M. opuntia* Roth, 1975; *M. rufocincta* (Newcomb, 1864). Anatomy described and illustrated: Pilsbry (1927, 1939), Roth (1975). Pearce (1990) analyzed shell morphometrics. Most species of *Micrarionta* have a dart sac and two mucus glands; these were entered as *Micrarionta*₁. *Micrarionta opuntia* lacks a dart sac and has only one mucus gland; this taxon was entered as *Micrarionta*₂.

Pilsbry (1927) found the dart sac absent in one dissection of *Micrarionta guadalupiana* (Pilsbry & Vanatta, 1898); in other specimens a well-developed dart sac was present. The two specimens I dissected both had fully developed dart sacs. I suspect that Pilsbry's first specimen was immature; in his figures, the mucus glands do not seem fully developed. Further sampling is needed.

Mohavelix Berry, 1943. Originally proposed as a subgenus of *Sonorella*; separated as a genus by Miller (1967a, 1968). Monotypic; type species *Micrarionta (Eremarionta) micrometalleus* Berry, 1930, examined. Anatomy described and illustrated by Berry (1943), Miller (1970).

Myotophallus Pilsbry, 1939. Originally proposed as a subgenus of *Sonorella*. Type species *Sonorella fragilis* Pilsbry, 1939. Taxa examined: *Sonorella (Myotophallus) rooseveltiana fragilis*; *S. (M.) rooseveltiana rooseveltiana* Berry, 1922; *S. (M.?) allynsmithi* Gregg & Miller, 1969. Anatomy described and illustrated: Pilsbry (1939), Miller (1967a), Gregg & Miller (1969), Bequaert & Miller (1973). *Sonorella rooseveltiana* was entered as terminal taxon *Myotophallus*₁. *Sonorella allynsmithi*, grouped by Bequaert

& Miller (1973) with *S. rooseveltiana*, differs in penial retractor insertion, presence of a minute verge, and other characters and was entered as *Myotophallus*₂.

Plesarionta Pilsbry, 1939. Originally proposed as a subgenus of *Micrarionta*; separated as a genus by Miller (1981c). Type species *Helix stearnsiana* Gabb, 1868. Species examined: *Plesarionta stearnsiana*, *P. orcutti* (Dall, 1900), *P. tryoni* (Newcomb, 1864). Anatomy described and illustrated: Pilsbry & Vanatta (1898), Pilsbry (1939), Roth (1982).

In *Plesarionta stearnsiana* the spermathecal diverticulum is very short or absent, both conditions sometimes occurring in a population. In the rest of the clade ((*Plesarionta*, *Xerarionta*), (*Greggelix*, *Martirelix*)), both the spermathecal diverticulum, which receives the spermatophore in copulation, and the epiphallic caecum, which secretes it, are extremely long, suggesting an "arms race" between competing male and female systems. The epiphallic caecum in *P. stearnsiana* is long. The short or absent spermathecal diverticulum implies a different way of managing the received spermatophore; I regard it as an autapomorphy of *P. stearnsiana*.

Rothelix Miller, 1985. Originally proposed as a subgenus of *Helminthoglypta*. Type species *Epiphragmophora cuyamacensis lowei* Bartsch, 1918. Species examined: *Helminthoglypta (Rothelix) lowei*, *H. (R.) cuyamacensis* Pilsbry, 1895; *H. (R.) rhodophila* Reeder & Miller, 1987; *H. (R.) warnerfontis* Reeder & Miller, 1988. Anatomy described and illustrated: Pilsbry (1939; see commentary by Miller, 1985), Miller (1985), Reeder & Miller (1987, 1988).

Sonorelix Berry, 1943. Type species *Micrarionta (Eremarionta) borregoensis* Berry, 1929. Species examined: *Sonorelix borregoensis*. Anatomy described and illustrated: Berry (1943), Miller (1972).

Sonorella binneyi group. Originally proposed by Pilsbry (1939) as an informal subdivision of *Sonorella* Pilsbry, 1900; content amended by Miller (1967a). Species examined: *Sonorella binneyi* Pilsbry & Ferriss, 1910; *S. xanthenes* Pilsbry & Ferriss, 1923; and *S. sitiens sitiens* Pilsbry & Ferriss, 1915; 23 other recognized species (Bequaert & Miller, 1973; Christensen & Reeder, 1981; Miller, 1984; Naranjo-García & Miller, 1986; Naranjo-García, 1988b, 1989) were not examined firsthand but are well documented in the literature. Anatomy described and illustrated: Pilsbry (1939), Miller (1966, 1967a, c, d, 1968, 1969, 1984), Christensen & Reeder (1981), Naranjo-García & Miller (1986), Naranjo-García (1988b, 1989).

A short spermathecal diverticulum occurs in one species, *Sonorella reederi* Miller, 1984. Miller (1984) regarded it as the renewed expression of genes usually masked in *Sonorella*. The diverticulum in *S. reederi* arises low on the spermathecal duct, which is capacious below the origin (Miller, 1984:fig. 2), whereas in other *Helminthoglyptidae* except *Sonorelix* it arises remote from the base of the spermathecal duct, and the duct below the origin is not dis-

tended. The diverticulum in *S. reederi* may not be homologous with those of other taxa.

Sonorella granulatissima group. Originally proposed by Pilsbry (1939) as an informal subdivision of *Sonorella*; content amended by Miller (1967a). Species examined: *Sonorella granulatissima* Pilsbry, 1905, and five of the 25 other recognized species (Bequaert & Miller, 1973; Fairbanks & Reeder, 1980; Naranjo-García, 1989). Anatomy described and illustrated: Pilsbry (1939), Miller (1967a, b, c), Fairbanks & Reeder (1980). This terminal taxon includes the type species of *Masculus* Pilsbry, 1939 (*Sonorella virilis* Pilsbry, 1905), and of *Sonoranax* Pilsbry, 1939 (*Sonorella dalli* Bartsch, 1904); both of these names are available for use when the group(s) containing the type species is (are) accorded formal taxonomic recognition.

Sonorella hachitana group. Originally proposed by Pilsbry (1939) as an informal subdivision of *Sonorella*; content amended by Miller (1967a). Species examined: *Sonorella hachitana* (Dall, 1896), and 13 of the 34 other recognized species (Bequaert & Miller, 1973; Gregg & Miller, 1974; Miller, 1976; Fairbanks & Reeder, 1980). Anatomy described and illustrated: Pilsbry (1939), Miller (1966, 1967a, b, 1968, 1976), Gregg & Miller (1974), Fairbanks & Reeder (1980), Naranjo-García (1988a). This terminal taxon includes the type species of *Sonorella* Pilsbry, 1900 (*S. hachitana*); *Sonorella, sensu stricto* is the valid name when the group is accorded formal taxonomic recognition as a subset of *Sonorella*.

Xerarionta Pilsbry, 1913. Originally proposed as a "section" of *Micrarionta*; separated as a genus by Miller (1981c). Type species *Arionta veitchii* 'Newcomb' Tryon, 1866 [= *Xerarionta levis canescens* (Adams & Reeve, 1848)]. Taxa examined: *Xerarionta levis canescens*; *X. areolata* (Pfeiffer, 1845); *X. kelletii* (Forbes, 1850), *X. pandorae* (Forbes, 1850). Anatomy described and illustrated: Pilsbry & Vanatta (1898), Pilsbry (1939), Miller (1972).

Taxa Excluded

Ariolimax Mörch, 1860. Type species *Limax columbianus* Gould in A. Binney, 1851. Webb (1961) assigned this genus of large slugs to Xanthonychidae (*sensu* Baker, 1959) because he found the verge of *A. columbianus* "to be structurally as in most xanthonychids [*sic*], except that the outer epithelial layer of the verge is more prominent. . . . The verge develops almost exactly as in xanthonychid snails" (Webb, 1961:34–35). These comparisons are in the form of a two-taxon statement; no comparison was made with the structure or development of verges in other families. Webb's further comments on the development of the genitalia compared *Monadenia* (of Bradybaenidae) and *Leptarionta* Fischer & Crosse, 1872 (of Humboldtianidae or Xanthonychidae, restricted), not any taxa of *Helminthoglyptidae* as construed herein. In *Ariolimax* the penial retractor is broad, inserting on the summit or side of the penis; the spermatheca has a short duct; a caudal mucus

pit and pronounced suprapedal grooves are present. I consider *Ariolimax* a genus of Arionoidea.

Cepolinae Ihering, 1909. Type genus *Cepolis* Montfort, 1810. In *Cepolis*, *Polymita* Beck, 1837, *Dialeuca* Albers, 1850, and *Setipellis* Pilsbry, 1926, a single globose mucus gland inserts on the summit of the dart sac, which in turn is seated on an atrial sac. A membrane encloses the atrial sac and other parts of the lower genitalia and bears a more or less bipartite gland consisting of numerous parallel tubules (Pilsbry, 1939; Baker, 1943). Webb's (1952a) observations on the structure of the mucus gland suggest that it is not homologous with the mucus bulbs of *Helminthoglypta*, as some authors suggested. Mucus glands inserting high on the dart sac are known in Xanthonychidae, restricted (e.g., *Metostracon* Pilsbry, 1900). No homology of the bipartite "sheath gland" with structures of the west American Helminthoglyptidae has been demonstrated. In *Cepolis* the seminal receptacle consists of a mass of tubercles; this condition has not been observed in Helminthoglyptidae as construed herein (Emberton, 1991). Nord-sieck (1987) regarded Cepolinae as distinct from Helminthoglyptinae; Miller & Naranjo-García (1991) allocated it to Xanthonychidae, restricted.

Gliabates Webb, 1959. Type species *G. oregonia* Webb, 1959. Webb (1959, 1961) tentatively referred this monotypic genus of slugs to Xanthonychidae (*sensu* Baker, 1959) without specifying the characters supporting that assignment. The reproductive system includes a small spermatheca on a short, broad duct, and a globose penial sac with a lobate internal collar forming upper and lower cavities. The penial retractor muscle inserts on the summit of the penis, separated from the epiphallus. No dart apparatus is present (G. R. Webb, written communication, 1990). There are no obvious synapomorphies with Helminthoglyptidae, and I regard *Gliabates* as a genus of Arionoidea.

Glypterpes Pilsbry, 1893. Type species *Helix veterna* Meek & Hayden, 1861, a Tertiary fossil. No anatomical information available.

Mesoglypterpes Yen, 1952. Type species *M. sagensis* Yen, 1952, a Cretaceous fossil. No anatomical information available.

Tryonigenis Pilsbry, 1927. Type species *Helix remondi* Tryon, 1863. Zilch (1960), followed by Miller (1967a), assigned this genus to Sonorellinae. Miller (1971) regarded it as more closely related to *Leptarionta*. Schileyko (1991) assigned it to a monotypic subfamily, Tryonigeninae, in Humboldtianidae. The short spermathecal duct, serrated dorsal keel, and smooth, practically unsculptured embryonic whorls are unlike anything in Helminthoglyptidae.

Characters

The data set consists of shell, integument, and reproductive system characters. Here are listed the characters,

character states, and hypothetical character-state trees, along with comments on specific characters used in the analysis.

1. Atrial sac (fingerlike lateral outpouching of genital atrium): (A) absent (all taxa but *Charodotes*, *Coyote*, *Helminthoglypta*₁, and *Rothelix*); (B) present, with vagina inserting near summit of atrial sac (*Rothelix*); (C) present, with vagina inserting on atrium at base of atrial sac (*Charodotes*, *Coyote*, *Helminthoglypta*₁). A → B → C.

Outgroup comparison establishes absence of the atrial sac as plesiomorphic; the copulatory pad in *Monadenia* is probably not homologous, involving as it does a much larger part of the lower genital tract. The atrial sac appears to develop through a process of progressive stripping off of the dart sac-bearing part of the vaginal wall. Character-state (B) represents an intermediate stage of the sequence from (A) to (C).

Webb (1952a) proposed the term "neophore" for the atrial sac and similar structures, with reference to their being newly evolved organs. Since "newness" (i.e., apomorphy) is relative to the ingroup under study, I retain the phylogenetically neutral term, atrial sac.

2. Mucus glands: (A) paired, inserting individually on vagina (*Chamaearionta*, *Eremarionta*₁, *Eremarionta*₂, *Micrarionta*₁, *Plesarionta*, *Xerarionta*); (B) paired, feeding into common duct that inserts at base of dart sac (*Charodotes*, *Coyote*, *Helminthoglypta*₁, *Helminthoglypta*₂, *Rothelix*); (C) single, fully developed (*Micrarionta*₂); (D) vestigial (either 1 or 2 present) (*Greggelix*, *Martirelix*). B ← A → C; A → D.

An additional character state, (E) mucus glands absent (*Eremariontoides*, *Herpeteros*, *Mohavelix*, *Myotophallus*₁, *Myotophallus*₂, *Sonorelix*, *Sonorella binneyi* group, *Sonorella granulatissima* group, *Sonorella hachitana* group) was not entered in the analysis but was mapped on the resulting tree. Outgroup comparison establishes mucus gland insertion on the vagina at or near the base of the dart sac as plesiomorphic.

3. Bulbous reservoirs on mucus gland ducts: (A) present (*Charodotes*, *Coyote*, *Eremarionta*₁, *Eremarionta*₂, *Helminthoglypta*₁, *Helminthoglypta*₂, *Rothelix*); (B) absent (all others; coded as "?" in taxa without mucus glands or ducts [2E, above]). B → A.

Small swellings on the mucus gland ducts in *Eremarionta rowelli* and *E. greggi* probably are homologous with the mucus bulbs in *Charodotes*, *Coyote*, *Helminthoglypta*, and *Rothelix*. This character was noticed in *Eremarionta* first by Schileyko (1991). The bulbs are thin-walled in *Helminthoglypta*₂ but more thickly and muscularly walled in *Charodotes*, *Coyote*, *Helminthoglypta*₁, and *Rothelix*, in which they probably play a more active rôle in mucus ejection.

4. Membranous mucus gland tissue: (A) enveloping lower genitalia (*Charodotes*, *Coyote*, *Helminthoglypta*₁, *Helminthoglypta*₂, *Rothelix*); (B) not enveloping lower genitalia (all others). B → A.

Development of membranous mucus glands is probably related to an increase in secretory surface area. (The same thing is accomplished in Helicidae by development of multiple tubules.) The extreme elaboration of the membranous surface (character state B) in *Helminthoglypta* and the taxa conventionally regarded as its subgenera is a continuation of this trend; the driving force may be sexual selection. Miller & Naranjo-García (1991:fig. 1) assumed that membranous glands were ancestral to vesicular glands and on that basis proposed the tree (Helminthoglyptidae, (Humboldtianidae, Xanthonychidae)). However, that phylogeny runs counter to the biogeographic history proposed in the same paper, in which Helminthoglyptidae and Xanthonychidae have a vicariant relationship related to the break-up of the ancient continent "Pacifica," while Humboldtianidae is indigenous to the North American craton.

5. Dart sac: (A) present, seated on vagina (*Chamaearionta*, *Eremarionta*₁, *Eremarionta*₂, *Helminthoglypta*₂, *Micrarionta*₁, *Plesarionta*, *Xerarionta*); (B) present, seated on atrial sac (*Charodotes*, *Coyote*, *Helminthoglypta*₁, *Rothelix*). A → B.

An additional character state, (C) dart sac absent (all other taxa) was not entered in the analysis but was mapped on the resulting tree.

Nordsieck (1987) used the term "Reizapparat" ("stimulatory organ") as a near synonym of "Pfeilapparat" (dart apparatus), and other authors have assumed that the function of the dart sac in courtship was stimulatory, but dart emplacement apparently has more to do with mediating male and female rôles in the mating of these simultaneous hermaphrodites (cf. Chung, 1987). I retain the neutral descriptive term, dart sac.

6. Spermathecal diverticulum: (A) absent (*Micrarionta*₁, *Micrarionta*₂, *Mohavelix*, *Myotophallus*₁, *Myotophallus*₂, *Sonorella binneyi* group, *Sonorella granulatisissima* group, *Sonorella hachitana* group); (B) of moderate length [0.7–2.0 times length of spermathecal duct above origin of diverticulum], arising well above base of spermathecal duct (*Charodotes*, *Coyote*, *Eremarionta*₂, *Eremariontoides*, *Helminthoglypta*₁, *Helminthoglypta*₂, *Martirelix*, *Rothelix*); (C) very long [>2.0 times length of spermathecal duct above origin of diverticulum], arising well above base of spermathecal duct (*Greggelix*, *Plesarionta*, *Xerarionta*); (D) of moderate length, arising near base of spermathecal duct (*Sonorelix*); (E) short [<0.7 times length of spermathecal duct above origin of diverticulum], arising well above base of spermathecal duct (*Chamaearionta*, *Eremarionta*₁, *Herpeteros*). A → B → C; A → D; B → E.

7. Muscular vaginal node: (A) present (*Sonorelix*); (B) absent (all others). B → A.

This character was first noticed by Miller (1972:134, fig. 2).

8. Epiphallic caecum: (A) of moderate length [0.3–2.0 times length of penis plus epiphallus] (*Charodotes*, *Coyote*, *Eremarionta*₁, *Eremarionta*₂, *Helminthoglypta*₁, *Helminthoglypta*₂, *Micrarionta*₁, *Micrarionta*₂, *Rothelix*, *Sono-*

relix); (B) minute [<0.15 times length of penis plus epiphallus], free from vas deferens (*Eremariontoides*, *Mohavelix*, *Myotophallus*₁, *Myotophallus*₂, *Sonorella binneyi* group, *Sonorella granulatisissima* group, *Sonorella hachitana* group); (C) very long [>2.0 times length of penis plus epiphallus] (*Greggelix*, *Martirelix*, *Plesarionta*, *Xerarionta*); (D) short [0.15–0.3 times length of penis plus epiphallus] (*Chamaearionta*, *Herpeteros*). A → B; A → C; A → D.

Monadenia has a moderately long epiphallic caecum. An epiphallic caecum that is minute and buried in connective tissues of the epiphallus occurs in three genera of Polygyridae—*Cryptomastix* Pilsbry, 1939; *Vespericola* Pilsbry, 1939; and *Hochbergellus* Roth & Miller, 1992; but the plesiomorphic condition in Polygyridae is an epiphallus without caecum (K. C. Emberton, personal communication, 1992).

9. Wall of lower portion of epiphallus: (A) single (all taxa but *Charodotes*, *Coyote*, *Eremarionta*₁, *Eremarionta*₂, *Helminthoglypta*, and *Rothelix*); (B) double; double-walled section more than $3/8$ (0.4 times) as long as penis, not extending into verge, cylindrical or club-shaped (*Charodotes*, *Helminthoglypta*₁, *Helminthoglypta*₂, *Rothelix*); (C) double; double-walled section less than $3/8$ (0.4 times) as long as penis, extending into verge at summit of penial chamber (*Eremarionta*₂); (D) double; double-walled section more than $3/8$ (0.4 times) as long as penis, extending into verge, conical, expanding to prominent swelling at lower end that projects into penial chamber as a short, broad papilla (*Eremarionta*₁, *Eremariontoides*); (E) double; double-walled section more than $3/8$ (0.4 times) as long as penis, not extending into verge, conical, expanding to prominent swelling at lower end that projects into penial chamber as a short, broad papilla (*Coyote*). A → B → C; B → D; B → E.

The portion of the male reproductive system in *Helminthoglypta* that has been called the preputial chamber (Gregg & Miller, 1976), the lower part of the penis (Miller, 1985), and the lower chamber of the penis (Reeder & Roth, 1988), is homologous with the penis of other genera, i.e., the saccular organ that is everted and performs intromission in mating. What has been called the penis (Gregg & Miller, 1976), the upper part of the penis (Miller, 1985), and the upper chamber of the penis (Reeder & Roth, 1988), is homologous with the lower portion of the epiphallus of other genera and is here referred to as such.

The transformation series proposed here (Figure 2) agrees with that of Schileyko (1991:194, fig. 4) in having the double walled condition originate above the verge. The fact that a double-walled lower portion of the epiphallus is widespread in *Eremarionta* was discovered in the course of this study; it was first depicted in Miller's (1981a:figs. 3C, 3D) figures of *E. greggi*.

10. Insertion of penial retractor muscle: (A) at or near base of epiphallus, close to or reaching summit of penis (*Herpeteros*, *Martirelix*, *Myotophallus*₁, *Sonorella binneyi* group; *Sonorella granulatisissima* group; *Sonorella hachitana*

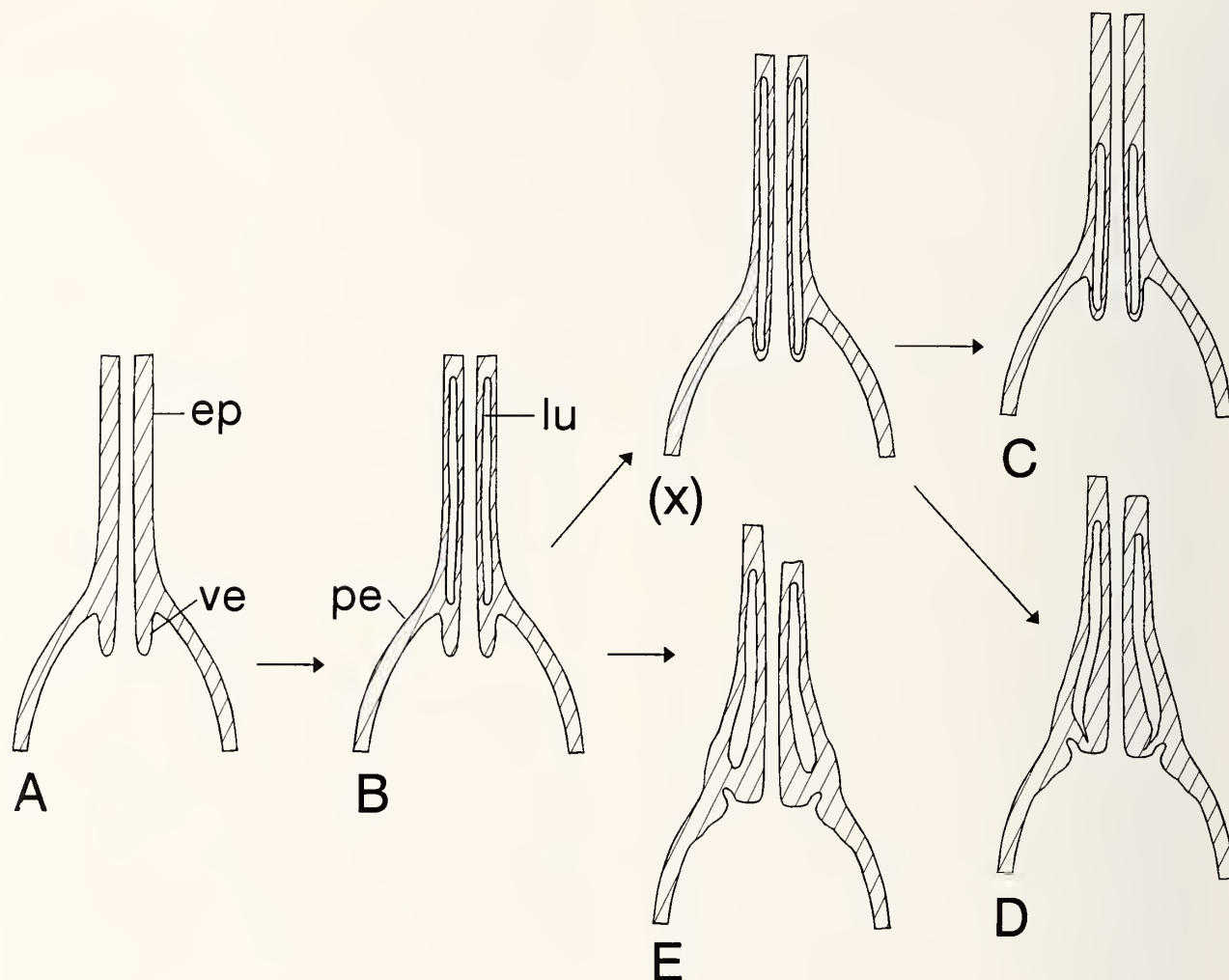


Figure 2

Diagrammatic lengthwise sections of lower portion of epiphallus and summit of penis showing transformation series for character 9. Abbreviations: ep, lower portion of epiphallus; lu, lumen of double-walled section of epiphallus; pe, summit of penis; ve, verge. (X) = intermediate grade with long lumen extending into verge.

group); (B) on epiphallus, remote from summit of penis (all others). B → A.

Outside of *Mytophallus*, and the *Sonorella* groups, a low insertion of the penial retractor muscle is associated with a large, heavy verge, possibly for reasons of mechanical efficiency.

11. Penial sac: (A) cylindrical to conic, single-chambered, without constriction setting off a separate chamber (all taxa but *Rothelix*); (B) sausage-shaped with post-medial constriction setting off a posterior chamber (*Rothelix*). A → B.

12. Verge: (A) roughly cylindrical or conic, small to medium-sized, occupying only upper end of penial sac, not markedly distending same (*Charodotes*, *Eremarionta*₂, *Helminthoglypta*₁, *Helminthoglypta*₂, *Mohavelix*, *Sonorelix*, *Sonorella binneyi* group); (B) minute or absent (*Chamae-*

arionta, *Mytophallus*₁, *Mytophallus*₂, *Rothelix*, *Xerarionta*); (C) consisting of a short, broad papilla developed from swelling of inner wall of double-walled lower portion of epiphallus (*Coyote*, *Eremarionta*₁, *Eremariontoides*); (D) roughly cylindrical or conic, very large, nearly filling swollen penial sac (*Herpeteros*); (E) broadly distending summit of penial sac, globose or hemispheric (*Greggelix*, *Micrarionta*₁, *Micrarionta*₂, *Plesarionta*); (F) broadly distending summit of penial sac, bullet-shaped to conical (*Martirelix*); (G) long, acicular, narrowly pointed, occupying much of length of penial sac (*Sonorella granulatissima* group, *Sonorella hachitana* group). A → B; A → C; A → D; A → E → F; A → G.

13. Penial sheath: (A) thin to moderately thick, not enveloping whole penis (*Sonorella binneyi* group, *Sonorella granulatissima* group, *Sonorella hachitana* group); (B) very

thick, enveloping whole penis (*Myotophallus*₁, *Myotophallus*₂); (C) absent (all others). B ← A → C.

The penial sheath in *Monadenia* is moderately thick, enveloping the basal part of the penis. The plesiomorphic condition in Polygyridae is a well-developed but not excessively thick sheath, enveloping the lower part of the penis (K. C. Emberton, personal communication, 1992).

14. Embryonic whorl sculpture: (A) radially wrinkled with overlay of sparse papillae, wrinkles usually weakly granulose (*Charodotes*, *Coyote*, *Greggelix*, *Helminthoglypta*₁, *Helminthoglypta*₂, *Herpeteros*, *Martirelix*, *Micrarionta*₁, *Micrarionta*₂, *Rothelix*); (B) first ≈ 0.5 whorl as in (A), thereafter papillose, papillae spirally elongated, discrete (*Chamaearionta*, *Eremarionta*₁, *Eremarionta*₂, *Eremariontoides*, *Myotophallus*₂); (C) first ≈ 0.5 whorl as in (A), thereafter papillose, papillae spirally elongated, confluent into network (*Mohavelix*, *Sonorelix*); (D) radially wrinkled, without overlay of papillae, wrinkles granulose (*Plesarionta*); (E) radially wrinkled, without overlay of papillae, wrinkles smooth (*Xerarionta*); (F) smooth or finely granulose, with spirally descending, sometimes divaricating, threads (*Myotophallus*₁, *Sonorella binneyi* group, *Sonorella hachitana* group); (G) coarsely granulose, with spirally descending, divaricating threads (*Sonorella granulatissima* group). C ← B → A → D → E; B → F → G.

In *Monadenia troglodytes* Hanna & Smith, 1933, sculpture of the first 0.25 whorl consists of wavy radial rugae with sparse, irregularly placed, round papillae. Over the next 0.5 whorl, the papillae become spirally elongated and tend to align in diagonal series; most of them remain discrete and do not fuse. Essentially the same pattern, character state (B), occurs in *Eremarionta*, *Eremariontoides*, and *Chamaearionta*; I hypothesize the origin of character state (A) by deletion of the elongation phase, and of character states (C), (F), and (G) by elaboration of it.

15. Shell color pattern: (A) including mottling and/or multiple banding (*Plesarionta*, *Xerarionta*); (B) not including mottling or multiple banding (all others). B → A.

16. Diagonal granulose sculpture on teleoconch: (A) present (*Xerarionta*); (B) absent (all others). B → A.

At least traces of diagonal granulose sculpture (Roth, 1984:fig. 32) occur in all species of *Xerarionta*, although they are faint and localized in some.

17. Malleation on teleoconch: (A) present (*Helminthoglypta*₁, *Helminthoglypta*₂, *Plesarionta*, *Xerarionta*); (B) absent (all others). B → A.

18. Papillation on teleoconch whorls: (A) absent (*Myotophallus*₁, *Plesarionta*, *Sonorella binneyi* group, *Sonorella hachitana* group, *Xerarionta*); (B) confined to spire, or mostly so (*Charodotes*, *Eremarionta*₁, *Eremarionta*₂, *Eremariontoides*, *Helminthoglypta*₁, *Helminthoglypta*₂, *Herpeteros*, *Micrarionta*₁, *Myotophallus*₂, *Rothelix*, *Sonorelix*); (C) extensive over shell, including body whorl (*Chamaearionta*, *Coyote*, *Greggelix*, *Martirelix*, *Micrarionta*₂, *Mohavelix*, *Sonorella granulatissima* group). A ← B → C.

19. Body whorl: (A) closely coiled [ratio of suture-to-periphery diameter of last whorl to diameter of adult shell

<0.23] (*Micrarionta*₁, *Micrarionta*₂); (B) not especially closely coiled [ratio of diameter of last whorl to diameter of adult shell ≥0.23] (all other taxa). B → A.

A ratio of < 0.23 occurs sporadically elsewhere as an autapomorphy (e.g., in some populations of *Helminthoglypta* (*Coyote*) *graniticola* Berry, 1926, and *Helminthoglypta* (*H.*) *arrosa* (W. G. Binney, 1858) and in *Plesarionta tryoni*); among other taxa the general range is 0.23 to 0.35.

20. Periostracum: (A) conspicuous (*Chamaearionta*, *Charodotes*, *Coyote*, *Helminthoglypta*₁, *Helminthoglypta*₂, *Mohavelix*, *Myotophallus*₁, *Myotophallus*₂, *Plesarionta*, *Rothelix*, *Sonorella binneyi* group, *Sonorella granulatissima* group, *Sonorella hachitana* group, *Xerarionta*); (B) inconspicuous to absent (*Eremarionta*₁, *Eremarionta*₂, *Eremariontoides*, *Greggelix*, *Herpeteros*, *Martirelix*, *Micrarionta*₁, *Micrarionta*₂, *Sonorelix*). A → B.

21. Body and mantle mucus: (A) highly colored (orange, yellowish, or chartreuse) (*Greggelix*, *Herpeteros*, *Martirelix*, *Sonorella binneyi* group, *Sonorella granulatissima* group, *Sonorella hachitana* group, *Myotophallus*₂); (B) colorless or milky (all other taxa). B → A.

Taxonomy

The results presented below document a partly nested, partly polytomous pattern of clades within the Helminthoglyptidae. This is sufficient to answer the questions posed by this study, but for systematists who would like to have the results expressed in the form of a list, I propose a taxonomy based on the following conventions. New taxon names are given phylogeny-based definitions in the Appendix.

In traditional biological taxonomy, taxon names are defined by lists of characters, regardless of whether the taxa are monophyletic, paraphyletic, or polyphyletic (de Queiroz & Gauthier, 1990). Decisions on naming or rank are often based on magnitude of difference criteria, recognizable by statements of the form, "[taxon X] is *different enough* from [taxon Y] that I recognize it as a [family, subfamily, etc.]" The phylogenetic taxonomy employed here uses three conventions not observed in traditional taxonomy: (1) no categorical ranks in the absolute sense are recognized; only relative rank, based on the phylogenetic hypothesis, with sister groups—the opposite branches of a fork in the tree—considered of equal dignity; (2) only monophyletic taxa are named, not paraphyletic or polyphyletic groups; and (3) monotypic groups are given no redundant names, except where necessary to keep an existing genus name from applying to a polyphyletic group (e.g., *Maricopella*, new genus for "*Sonorella*" *allynsmithi*). These conventions are more fully expounded by Gauthier et al. (1988). The names of previously recognized groups that are paraphyletic according to this analysis are enclosed in quotation marks.

The system proposed here intersects the traditional classification at two points: the most inclusive taxon retains the familiar name Helminthoglyptidae, not to express cat-

Table 2

Six maximally parsimonious trees based on analysis of data in Table 1.

Tree 1
 (OUT,(MY2,(MY1,(SNB,(SNG,SNH))),((MOH,SLX),((MI1,MI2),((CHM,HER),((GRE,MAR),(PLE,XER))),((ER2,(ER1,ERO)),(HL2,(ROX,(CHR,COY,HL1))))))))))

Tree 2
 (OUT,(MY2,((MY1,SNB),(SNG,SNH))),((MOH,SLX),(MI1,MI2),((CHM,HER),((GRE,MAR),(PLE,XER))),((ER2,(ER1,ERO)),(HL2,(ROX,(CHR,COY,HL1))))))))))

Tree 3
 (OUT,(MY2,(MY1,(SNB,(SNG,SNH))),((MOH,SLX),((MI1,MI2),(((GRE,MAR),(PLE,XER)),((CHM,HER),((ER2,(ER1,ERO)),(HL2,(ROX,(CHR,COY,HL1))))))))))))))

Tree 4
 (OUT,(MY2,(MY1,SNB),(SNG,SNH))),((MOH,SLX),((MI1,MI2),((CHM,HER),((GRE,MAR),(PLE,XER))),((ER2,(ER1,ERO)),(HL2,(ROX,(CHR,COY,HL1))))))))))

Tree 5
 (OUT,(MY2,((MY1,SNB),(SNG,SNH))),((MOH,SLX),((MI1,MI2),(((GRE,MAR),(PLE,XER)),((CHM,HER),((ER2,(ER1,ERO)),(HL2,(ROX,(CHR,COY,HL1))))))))))))))

Tree 6
 (OUT,(MY2,(MY1,SNB),(SNG,SNH))),((MOH,SLX),((MI1,MI2),(((GRE,MAR),(PLE,XER)),((CHM,HER),((ER2,(ER1,ERO)),(HL2,(ROX,(CHR,COY,HL1))))))))))))))

egorical rank but simply as a link to the traditional classification of pulmonate land snails. At the other end, I continue to use Latin binomina (set in italics) for the lowest, least inclusive taxa—species; I am not prepared to deal with the confusion that would result from abandoning ICZN Article 5.⁴ However, for many of the generic names themselves, I introduce a global conversion according to the following formula: [genus-name] is defined as [type species of the genus] and all taxa that share a more recent common ancestor with it than with [name of sister group] (see Appendix). This form of definition is consistent with the International Code of Zoological Nomenclature, which specifies that a genus is defined by reference to its type species—as is the case here—but does not dictate the basis for assigning other species to a genus. Between these two tie points, the traditional formal suffixes, with their imputations of rank (-ini, “tribe”; -inae, “subfamily”) are not used.

One typographical convention is introduced: the names of taxa that have phylogeny-based definitions (or are used with regard to their phylogeny-based definitions, if more than one definition exists) are set in SMALL CAPITAL LETTERS.

⁴ The so-called binominal system is in practice trinominal—genus, subgenus, and species—with a built-in three-tiered hierarchy of ranks. Not renaming the second level of taxa in clades with unresolved terminal polytomies (HELMINTHOGLYPTA) or numerous species (SONORELLA), but allowing the existing genus names to stand, nomenclaturally forces the subordinate terminal taxa into the rank of subgenus. This is in keeping with current usage and leaves the finer resolution to monographers of those genera. A wholly rank-free taxonomy would not utilize subgenera as such. I have steered a middle course that preserves many familiar names in their customary sense for the time being.

This convention may have wider use in papers in which it is necessary to discuss both taxa with and without phylogeny-based definitions. Where I use an existing genus name in the sense implied by its phylogenetic redefinition, the name is set in small capitals; otherwise, it is set in italics.

RESULTS

The analysis produced 377 maximally parsimonious trees 76 steps in length, with consistency index 0.57, and retention index (Farris, 1989) 0.73. Iterations of the successive approximations weighting and branch-breaking procedures reduced the number of trees to six. Table 2 presents these trees in parenthetical notation. They differ from one another principally as shown in Figure 3. The strict consensus tree is shown in Figure 4. It is 76 steps long with consistency index 0.57 and retention index 0.73. This tree is used as the basis for the following taxonomy of Helminthoglyptidae. Because a consensus tree represents the information on grouping shared by all the competing cladograms, it is less resolved than any, and a taxonomy based on it should be viewed as conservative (Carpenter, 1988).

In the proposed taxonomy (Table 3), hierarchic relations among the taxa are indicated by successive indentation.⁵

⁵ A hypothetical systematist concerned with expressing these results within the Linnaean hierarchy would probably adopt the following measures: (1) call HELMINTHOGLYPTAMORPHA and SONORELLAMORPHA, primary subdivisions of the Helminthoglyptidae, “Helminthoglyptinae” (the earliest-proposed existing family-group name typologically based on an included taxon) and “Sonorellinae,” respectively, or, with equally good reason, “Hel-

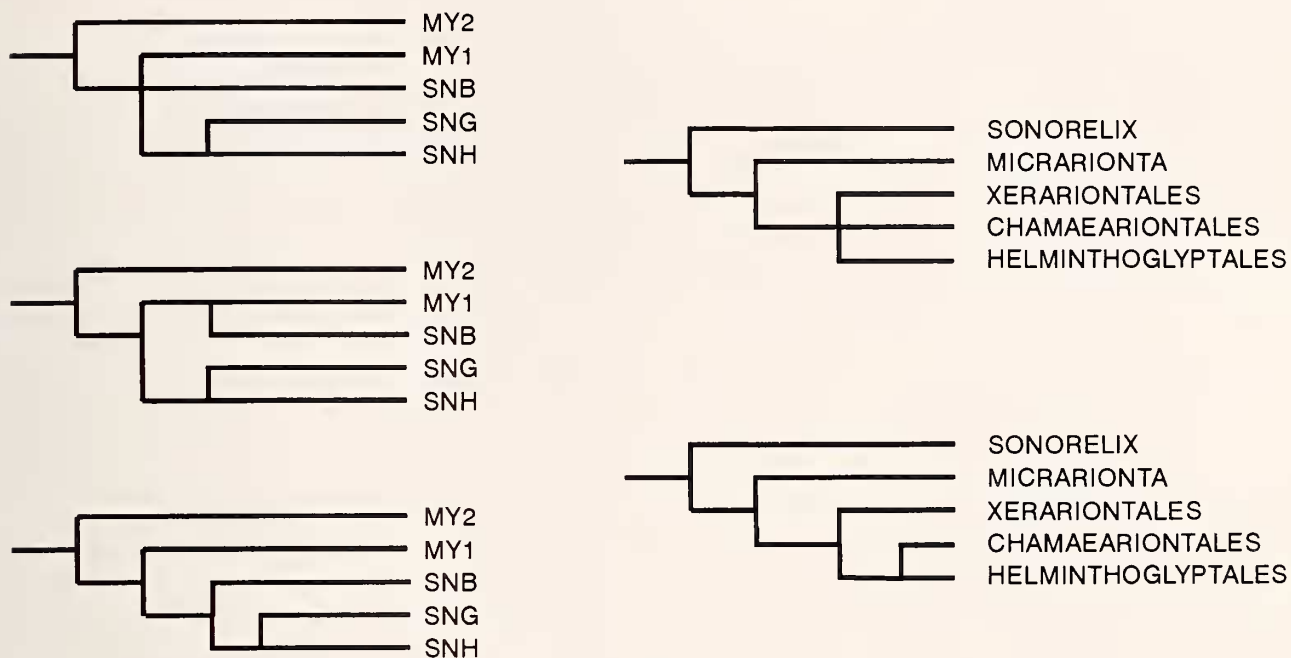


Figure 3

Differing components of trees in Table 2; left, in SONORELLAMORPHA (abbreviations as in Table 1); right, in HELMINTHOGLYPTAMORPHA (taxa defined in following text).

Table 4 compares the content of taxa proposed in this paper to the taxa recognized by Nordsieck (1987) and Schileyko (1991).

The tree exhibits a basal trichotomy among the outgroup, the taxa conventionally assigned to *Sonorella* (SONORELLAMORPHA), and the rest of the Helminthoglyptidae (HELMINTHOGLYPTAMORPHA). SONORELLAMORPHA is diagnosed by the synapomorphies of minute epiphallid caecum (character state 8B) (homoplastic in *Eremariontoides argus*) and colored mucus (21A). Mucus glands and dart sac are absent (2E, 5C). As discussed below, whether these absences are considered apomorphic or plesiomorphic depends on interpretation of the outgroup.

minthoglyptidae" and "Sonorellidae"; (2) call CHAMAEARIONTALES, XERARIONTALES, and HELMINTHOGLYPTALES (major subdivisions of "Helminthoglyptinae"), "Chamaeariontini," "Xerariontini," and "Helminthoglyptini," and (3) interpose taxa named "Sonorelicini" and "Micrariontini" hierarchically between SONORELIX and "Helminthoglyptinae" and MICRARIONTA and "Helminthoglyptinae," respectively. I reject measures (1) and (2) because in the Linnaean system the suffixes -inae and -ini denote formal categorical ranks. There is no reason having to do with the biology or evolutionary history of the organisms why those names could not equally well be applied to other subdivisions containing their nominotypical genera. Any such decision is subjective and arbitrary. Measure (3) runs counter to the convention of no redundant names: "Sonorelicini" and SONORELIX would have identical membership, as would "Micrariontini" and MICRARIONTA.

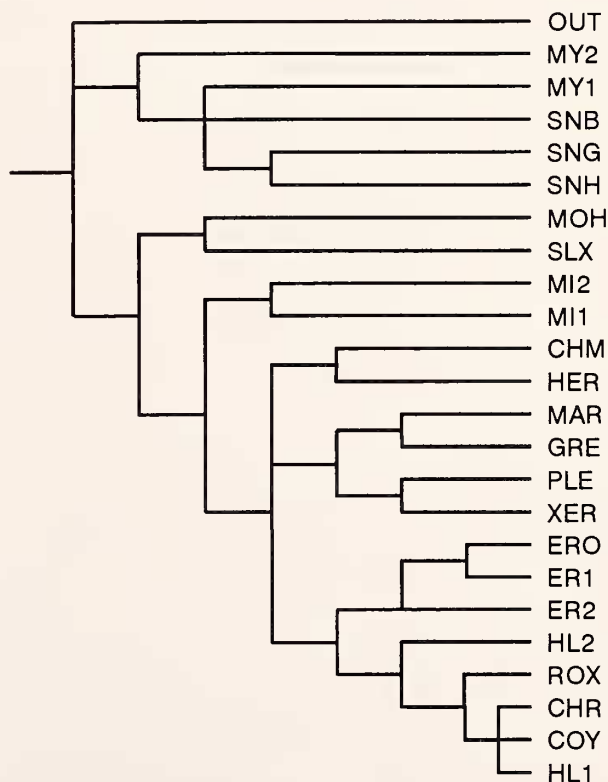


Figure 4

Strict consensus tree for taxa of Helminthoglyptidae. Abbreviations as in Table 1.

Table 3

Phylogenetic taxonomy of the Helminthoglyptidae.

HELMINTHOGLYPTIDAE
SONORELLAMORPHA
<i>Maricopella allynsmithi</i>
SONORELLALES
MYOTOPHALLUS
"Sonorella binneyi group"
SONORELLA
SONORANAX (<i>Sonorella granulatissima</i> group)
"Sonorella, sensu stricto"
HELMINTHOGLYPTAMORPHA
SONORELIX
<i>Mohavelix micrometalleus</i>
SONORELIX, SENSU STRICTO
HELMINTHOGLYPTAINA
MICRARIONTA
NICOLENEA
MICRARIONTA, SENSU STRICTO
HELMINTHOGLYPTOTES
CHAMAEARIONTALES
<i>Chamaearionta aquaealbae</i>
HERPETEROS
XERARIONTALES
GREGGELIX
MARTIRELIX
"Greggelix, sensu stricto"
XERARIONTA
XERARIONTA, SENSU STRICTO
"Plsarionta"
HELMINTHOGLYPTALES
EREMARIONTAPHIM
CAHULLUS
EREMARIONTA
<i>Eremariontoides argus</i>
EREMARIONTA, SENSU STRICTO
HELMINTHOGLYPTAPHIM
<i>Noyo intersessa</i>
HELMINTHOGLYPTANIKI
ROTHELIX
HELMINTHOGLYPTA
<i>Helminthoglypta, sensu stricto</i>
Coyote
"Charodotes"

SONORELLAMORPHA consists of two primary component clades. The first, *Maricopella allynsmithi* (that is, *Myotophallus*₂ of the preceding data set), is diagnosed by minute verge (12B) (homoplastically derived in XERARIONTA, SENSU STRICTO and ROTHELIX) and thick penial sheath enveloping the whole penis (13B). A thick penial sheath is either homoplastically derived in *Myotophallus* or reversed in other SONORELLALES. The second primary component clade, SONORELLALES, is diagnosed by penial retractor inserting at base of epiphallus (10A) (homoplastically derived in HERPETEROS and MARTIRELIX); embryonic whorl sculpture of spirally descending, sometimes divaricating threads (14F); and general absence of papillation on the teleoconch whorls (18A) (also occurring

in XERARIONTA; reversed in the *Sonorella granulatissima* group).

The component taxa of SONORELLALES plot as an unresolved trichotomy: MYOTOPHALLUS (that is, *Myotophallus*₁), diagnosed by thick penial sheath enveloping the whole penis (13B), the (homoplastic) absence of a verge (12B), and colorless mucus (21B) (a reversal); the "*Sonorella binneyi* group," which has no autapomorphies in the present phylogenetic hypothesis and is regarded as paraphyletic pending further study; and SONORELLA, diagnosed by a long, acicular verge (12G). SONORELLA consists of two subclades. The *Sonorella granulatissima* group is diagnosed by embryonic whorls coarsely granulose with spirally descending, divaricating threads (14G) and extensive papillation (18C) (homoplastically derived in several clades of HELMINTHOGLYPTAMORPHA). This clade contains the type species of SONORANAX, and I apply that name, in its phylogeny-based definition, to it. Whether *Masculus* is useful as the name for a component clade of SONORANAX will depend on the results of a monographic study of the species of the group. The second subclade, "*Sonorella, sensu stricto*," has no autapomorphies in the present phylogenetic hypothesis and is regarded as paraphyletic pending further study.

HELMINTHOGLYPTAMORPHA is diagnosed by the absence of a penial sheath (13C). The periostracum is greatly reduced or absent on the teleoconch (20B), but this transformation shows at least one reversal in every principal clade of HELMINTHOGLYPTAMORPHA except MICRARIONTA, often in combination with other character states implying progenesis.

HELMINTHOGLYPTAMORPHA consists of two primary component clades. The first, SONORELIX, is diagnosed by netlike embryonic whorl sculpture (14C). Mucus glands and dart sac are absent (2E, 5C). SONORELIX consists of two subclades. The monotypic *Mohavelix micrometalleus* is diagnosed by a minute epiphallic caecum (8B), extensive papillation (18C), and a conspicuous periostracum (20A; a reversal). These apomorphies also occur elsewhere in HELMINTHOGLYPTAMORPHA. SONORELIX, SENSU STRICTO is diagnosed by the presence of a vaginal node (7A) and a spermathecal diverticulum in a basal position.

The second primary component clade of HELMINTHOGLYPTAMORPHA, HELMINTHOGLYPTAINA, is diagnosed by embryonic whorl sculpture of radial wrinkles overlain by sparse papillae (14A). HELMINTHOGLYPTAINA consists of two component clades. The first, MICRARIONTA, is diagnosed by globose verge (12E) (homoplastic in XERARIONTALES) and close coiling (19A). MICRARIONTA consists of two subclades. NICOLENEA, new subgenus (that is, *Micrarionta*₂), is diagnosed by absence of descending mucus gland and dart sac (2C, 5C) and extensive papillation (18C). MICRARIONTA, SENSU STRICTO (that is, *Micrarionta*₁) has no autapomorphies in the present data set. Pearce's (1990) cladistic analysis resolved a clade consisting of *Micrarionta facta* and six other species as the sister group of the clade here designated NICOLENEA. It

Table 4

Relationship of content of taxa of phylogenetic taxonomy proposed in this paper and classifications of Nordsieck (1987) and Schileyko (1991). Order of taxa same as in Table 3. Note that upon further analysis the membership (and hence the equivalence) of taxa of the phylogenetic system could change without the taxon definitions changing.

This paper	Nordsieck (1987) ¹	Schileyko (1991)
HELMINTHOGLYPTIDAE	Helminthoglyptinae	Helminthoglyptidae in part + Xanthonychidae in part
SONORELLAMORPHA	"Sonorella-Gruppe" (of Sonorellini) (in part?)	Sonorellinae (of Xanthonychidae) in part
<i>Maricopella allynsmithi</i>	not treated	not treated
SONORELLALES	["Sonorella-Gruppe" in part]	Sonorellinae in part
<i>Myotophallus</i>	["Sonorella-Gruppe" in part]	Sonorellinae in part
"Sonorella binneyi group"	["Sonorella-Gruppe" in part]	Sonorellinae in part
SONORELLA	"Sonorella-Gruppe" in part	Sonorellinae in part
SONORANAX	["Sonorella-Gruppe" in part]	Sonorellinae in part
"Sonorella, sensu stricto"	"Sonorella-Gruppe" in part	Sonorellinae in part
HELMINTHOGLYPTAMORPHA	Helminthoglyptini + "Sonorella-Gruppe" in part?	Helminthoglyptidae in part + Xanthonychidae in part
SONORELIX	"Sonorella-Gruppe" in part?	Sonorellinae in part
<i>Mohavelix micrometalleus</i>	not treated	Sonorellinae in part (as <i>Mohavelix</i>)
SONORELIX, SENSU STRICTO	"Sonorella-Gruppe" in part?	Sonorellinae in part
HELMINTHOGLYPTAINA	Helminthoglyptini	Helminthoglyptinae + Eremariontinae + Micrariontinae (of Xanthonychidae) + Sonorellinae in part
MICRARIONTA	"Micrarionta-Gruppe" (of Helminthoglyptini) in part	Micrariontinae in part
NICOLENEA	not treated	not treated
MICRARIONTA, SENSU STRICTO	"Micrarionta-Gruppe" in part	Micrariontinae in part
HELMINTHOGLYPTOTES	Helminthoglyptini in part	Helminthoglyptinae + Eremariontinae + Micrariontinae in part + Sonorellinae in part
CHAMAEARIONTALES	[Helminthoglyptini in part]	not treated
<i>Chamaearionta aquaealbae</i>	["Micrarionta-Gruppe" in part]	not treated
HERPETEROS	not treated	not treated
XERARIONTALES	Helminthoglyptini in part	Micrariontinae in part + Sonorellinae in part
GREGGELIX	Helminthoglyptini in part	Sonorellinae in part
MARTIRELIX	not treated	not treated
"Greggelix, sensu stricto"	Helminthoglyptini in part	Sonorellinae in part
XERARIONTA	["Micrarionta-Gruppe" in part]	Micrariontinae in part
XERARIONTA, SENSU STRICTO	["Micrarionta-Gruppe" in part]	Micrariontinae in part
"Plesarionta"	["Micrarionta-Gruppe" in part]	Micrariontinae in part
HELMINTHOGLYPTALES	Helminthoglyptini in part	Helminthoglyptidae + Sonorellinae in part
EREMARIONTAPHIM	["Micrarionta-Gruppe" in part]	Eremariontinae + Sonorellinae in part
CAHULLUS	not treated	not treated
EREMARIONTA	["Micrarionta-Gruppe" in part]	Eremariontinae in part + Sonorellinae in part
<i>Eremariontoides argus</i>	not treated	Sonorellinae in part (as <i>Eremariontoides</i>)
EREMARIONTA, SENSU STRICTO	["Micrarionta-Gruppe" in part]	Eremariontinae in part
HELMINTHOGLYPTAPHIM	Helminthoglyptini in part	Helminthoglyptinae
<i>Noyo intersessa</i>	not treated	not treated
HELMINTHOGLYPTANIKI	<i>Helminthoglypta</i> in part	Helminthoglyptinae in part
ROTHELIX	[<i>Helminthoglypta</i> in part]	<i>Helminthoglypta</i> in part
HELMINTHOGLYPTA	<i>Helminthoglypta</i> in part	Helminthoglyptinae in part
<i>Helminthoglypta, sensu stricto</i>	<i>Helminthoglypta</i> in part	<i>Helminthoglypta</i> in part
<i>Coyote</i>	[<i>Helminthoglypta</i> in part]	<i>Helminthoglypta</i> in part
"Charodotes"	[<i>Helminthoglypta</i> in part]	<i>Helminthoglypta</i> in part

¹ The "Micrarionta-Gruppe" of Nordsieck (1987) is assumed to include the taxa that Pilsbry (1939) treated as subgenera of *Micrarionta*. Bracketed equivalences are inferred.

was defined by five measurements and ratios of the shell lip, lip convexity, and the presence of spiral lines on the shell. Lip convexity and one ratio show reversals within the clade. The other character states are synapomorphic with respect to the array of taxa considered. I accept this clade provisionally as MICRARIONTA, SENSU STRICTO pending further study. On Pearce's (1990:fig. 7) consensus tree, *Micrarionta guadalupiana* is the sister group of (NICOLENEA, MICRARIONTA SENSU STRICTO) but is paraphyletic, without a defining autapomorphy in the Pearce hypothesis.

The second component clade of HELMINTHOGLYPTAINA, HELMINTHOGLYPTOTES, is diagnosed by a spermathecal diverticulum of moderate length (6B). It consists of three primary component clades. The first, CHAMAEARIONTALES, is diagnosed by short epiphallic caecum (6E) and short spermathecal diverticulum (8D). CHAMAEARIONTALES consists of two subclades. The monotypic *Chamaearionta aquaealbae* is diagnosed by the absence of a verge (12B), extensive papillation (18C), and a conspicuous periostracum (20A; a reversal). These apomorphies also occur elsewhere in HELMINTHOGLYPTAMORPHA. The second subclade, HERPETEROS, is diagnosed by the absence of mucus glands and dart sac (2E, 5C), penial retractor inserting at base of epiphallus (10A), very large verge (12D), and embryonic whorl sculpture of radial wrinkles overlain by sparse papillae (14A). All except (12D) are homoplastic elsewhere in HELMINTHOGLYPTAMORPHA.

The second primary component clade of HELMINTHOGLYPTOTES, XERARIONTALES, is diagnosed by a very long epiphallic caecum (8C) (partly reversed in MARTIRELIX) and probably by a very long spermathecal diverticulum (6C) (also partly reversed in MARTIRELIX). In an equally parsimonious alternative interpretation, a long spermathecal diverticulum could have originated twice, in "*Greggelix, sensu stricto*" and in XERARIONTA. I favor the former interpretation, in which the transformations of spermathecal diverticulum and epiphallic caecum are correlated.

XERARIONTALES consists of two subclades. GREGGELIX is diagnosed by vestigial mucus glands (2D) (lost in some species of "*Greggelix, sensu stricto*"), absence of a dart sac (5C), extensive papillation (18C) (homoplastic), and colored mucus (21A) (also occurring in SONORELLAMORPHA). GREGGELIX consists of two subclades. MARTIRELIX is diagnosed by penial retractor inserting at base of epiphallus (10A) (homoplastic in HERPETEROS and SONORELLAMORPHA), bullet-shaped to conical verge (12F), and moderately long spermathecal diverticulum (6B) (a probable reversal). Unless a very long spermathecal diverticulum (6C) is considered to have originated anew, homoplastically with that in XERARIONTA, the second subclade, "*Greggelix, sensu stricto*," has no autapomorphies in this phylogenetic hypothesis and is regarded as paraphyletic pending further study.

The second subclade of XERARIONTALES, XERARIONTA, is diagnosed by mottling or multiple banding (15A), malleation (17A) (homoplastic in *Helminthoglypta, sensu stricto*

and *Noyo intersessa* [that is, *Helminthoglypta*₂]), and embryonic whorl sculpture of radial wrinkles without an overlay of papillae (14D); papillation is absent from teleoconch whorls (18A) (homoplastic in SONORELLALES). XERARIONTA consists of two subclades. XERARIONTA, SENSU STRICTO is diagnosed by smooth embryonic whorl wrinkles (14E), diagonal granulose sculpture (16A), and the (homoplastic) absence of a verge (12B). "*Plesarionta*" has no autapomorphies in this phylogenetic hypothesis and is regarded as paraphyletic pending further study.

The third primary component clade of HELMINTHOGLYPTOTES, HELMINTHOGLYPTALES, is diagnosed by bulbous mucus gland reservoirs (3A) (secondarily lost in *Eremariontoides argus*) and the double wall of the lower part of the epiphallus (9B). HELMINTHOGLYPTALES consists of two subclades. EREMARIONTAPHIM is diagnosed by embryonic whorl sculpture of spirally elongated, discrete papillae (14B; a reversal); it also shows extension of the double-walled section of the epiphallus into the verge, a component in common of states 9C and 9D. EREMARIONTAPHIM consists of two subclades. CAHULLUS, new genus (that is, *Eremarionta*₂), is diagnosed by a double-walled section of the epiphallus less than 0.4 times the length of the penis (9C). EREMARIONTA is diagnosed by a conical double-walled section of the epiphallus (9D) and a short, broad, papillar verge (12C) (homoplastic with that in *Coyote*). EREMARIONTA consists of two subclades. *Eremariontoides argus* is diagnosed by the absence of mucus glands and dart sac (2E, 5C) and by minute epiphallic caecum (8B) (homoplastic in SONORELLAMORPHA and *Mohavelix micrometalleus*). EREMARIONTA, SENSU STRICTO (that is, *Eremarionta*₁) is diagnosed by a short spermathecal diverticulum (6E) (homoplastic in CHAMAEARIONTALES).

The second subclade of HELMINTHOGLYPTALES, HELMINTHOGLYPTAPHIM, is diagnosed by the common duct of the mucus glands (2B), membranous tissue enveloping the lower genitalia (4A), embryonic whorl sculpture of radial wrinkles overlain by sparse papillae (14A) (also occurring in HERPETEROS and MICRARIONTALES), and the presence of a conspicuous periostracum (20A; a reversal). HELMINTHOGLYPTAPHIM consists of two subclades. *Noyo intersessa* (that is, *Helminthoglypta*₂) is diagnosed by the presence of malleation on the teleoconch (17A) (homoplastic in *Helminthoglypta, sensu stricto*, and XERARIONTA). Malleation apparently tends to be associated with large, more or less globose, capacious-whorled shells and is evidently not a good indicator of phylogeny in this context. HELMINTHOGLYPTANIKI is diagnosed by the presence of an atrial sac (1B), with the dart sac seated on it (5B).

HELMINTHOGLYPTANIKI consists of two subclades. ROTHELIX is diagnosed by penial chamber with post-medial constriction (11B) and the (widely homoplastic) absence of a verge (12B). HELMINTHOGLYPTA is diagnosed by vagina inserting on atrium at base of atrial sac (1C). The component taxa of HELMINTHOGLYPTA plot as an unresolved trichotomy: *Helminthoglypta, sensu stricto*, diagnosed by malleation (17A) (homoplastic in XERARIONTA

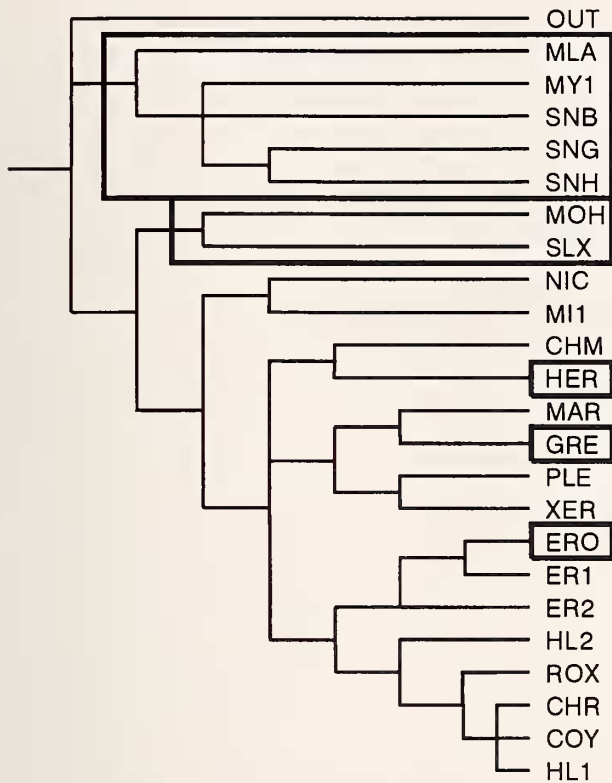


Figure 5

Absence of mucus glands mapped on consensus tree. Abbreviations as in Table 1, except for new taxa: MLA, *Maricopella allynsmithi*; NIC, NICOLENEA; CAH, CAHULLUS; NOY, *Noyo intersessa*. Absence is variable in GREGGELIX.

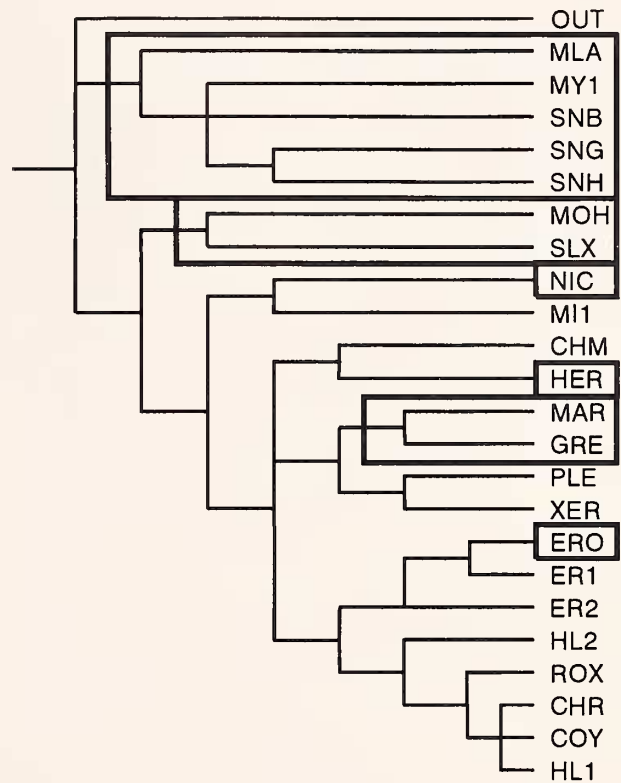


Figure 6

Absence of dart sac mapped on consensus tree. Abbreviations as in Figure 5.

and *Noyo intersessa*); *Coyote*, diagnosed by conical double-walled section of epiphallus (9E) and papillar verge (12C) (homoplastically derived in EREMARIONTA); and “*Charodotes*,” which has no autapomorphies in the present phylogenetic hypothesis and is regarded as paraphyletic pending further study. A verge is absent homoplastically in some species of “*Charodotes*” and *Helminthoglypta, sensu stricto*. Phylogeny-based definitions of the component taxa of HELMINTHOGLYPTA are left for a monographic study of the group.

Figure 5 plots the distribution of the total absence of mucus glands (2E) on the consensus tree. This character state occurs as an apomorphy in SONORELLAMORPHA, HERPETEROS, SONORELIX, *Eremariontoides argus*, and some species of “*Greggelix, sensu stricto*.” If the absence in SONORELLAMORPHA is accepted as due to loss, a minimum of five independent origins of the condition is indicated.

Figure 6 plots the distribution of the absence of dart sac (5C) on the consensus tree. This character state occurs as an apomorphy in SONORELLAMORPHA, HERPETEROS, SONORELIX, NICOLENEA, GREGGELIX, and *Eremariontoides argus*. If the absence in SONORELLAMORPHA is accepted as

due to loss, a minimum of six independent, homoplastic origins of the condition is indicated.

DISCUSSION

This analysis falsifies the proposition that absence of dart sac and/or mucus glands originated only once (Schileyko, 1991) as the most parsimonious account of helminthoglyptid evolution. It provides evidence against most other ancestor-descendant relationships suggested by previous authors.

All the taxa of HELMINTHOGLYPTAMORPHA have apomorphies (including the synapomorphic absence of penial sheath) that eliminate them as potential ancestors of the taxa of SONORELLAMORPHA.

Maricopella allynsmithi is the sister group of all other taxa conventionally referred to *Sonorella* (that is, of SONORELLALES), but the autapomorphies of minute verge (12B) and thick penial sheath (13B) rule it out as “a relatively unchanged descendant of the ancestral *Sonorella* founder” (Gregg & Miller, 1969:92). Its similarities to EREMARIONTA are symplesiomorphies.

Embryonic whorl sculpture (14C) and the absence of mucus glands (2E) support *Mohavelix micrometalleus* as the sister group of SONORELIX, SENSU STRICTO rather than

of *Helminthoglypta micrometalleoides* as Miller (1970) suggested.

GREGGELIX is the sister group of XERARIONTA, not the derivative of any population assignable to XERARIONTA as surmised by Miller (1972).

Eremariontoides argus is the sister group of EREMARIONTA SENSU STRICTO. This relationship rules out the simple common ancestry with "*Eremarionta*" *greggi* suggested by Miller (1981a); based on the moderately long spermathecal diverticulum and conic verge, "*E.*" *greggi* is a species of CAHUILLUS.

Roth (1987b) stated that in *Noyo intersessa* the muscularized common duct of the mucus glands had (apomorphically) taken over the function of mucus ejection performed by muscular mucus bulbs in most species of *Helminthoglypta*. The present phylogenetic hypothesis indicates that the muscular common duct and thin-walled mucus bulbs of *N. intersessa* are plesiomorphic with respect to the muscular bulbs and slender common duct in HELMINTHOGLYPTANIKI.

ROTHELIX, regarded by all previous authors as a subgenus of *Helminthoglypta*, is the sister group of all other taxa conventionally assigned to *Helminthoglypta*. Its position on the consensus tree does not suggest recent evolution from "an [*Helminthoglypta*]. *traskii*-like ancestor" (Miller, 1985) but rather an origin preceding the radiation of HELMINTHOGLYPTA into its component clades. It preserves an intermediate state in the stripping off of the atrial sac from the vagina (1B). At the same time, the male system shows the apomorphies of a post-medial constriction setting off a posterior chamber of the penial sac and the absence of a verge.

The differences between my results and those of Pearce (1990) and Schileyko (1991) are adequately accounted for by character coding and argumentation (in the case of Pearce) and method (in the case of Schileyko), and will not be belabored here.

Since Pilsbry's (1939) monograph, the taxa here assigned to SONORELLAMORPHA have been regarded as secondarily simplified from a dart-bearing ancestor. However, SONORELLAMORPHA is a basal clade, the sister group of HELMINTHOGLYPTAMORPHA, and not derivable from any other clade of Helminthoglyptidae. SONORELLAMORPHA and HELMINTHOGLYPTAMORPHA share no common ancestor not also shared by the presumptive sister group (Xanthonychidae, Bradybaenidae). If the taxa of SONORELLAMORPHA are in fact secondarily simplified, they may as readily have lost a xanthonychid-bradybaenid type of dart apparatus as a helminthoglyptid type. Or they may never have had one. If Polygyridae is regarded as the outgroup (which does not greatly affect the structure of the consensus tree) then absence of dart apparatus in SONORELLAMORPHA is plesiomorphic. Therefore, the monophyly of Helminthoglyptidae of authors (e.g., Miller & Naranjo-García, 1991) remains open to question, and more information is needed to determine whether SONORELLAMORPHA is contained within HELMINTHOGLYPTIDAE as defined herein.

The use of fossils to calibrate a phylogeny in time, especially one as strongly based on soft anatomical characters as this one, is not without risks. The situation is made worse by the rampant parallelism and convergence in shell form among land snails. I accept the following generic identifications, which constrain the time scale of helminthoglyptid evolution. *Xerarionta waltmilleri* Roth, 1984, from the Vieja Group of Trans-Pecos Texas, is between 39.6 and 37.7 Ma (late Eocene) in age (Roth, 1984). It shows the diagonal granulose sculpture diagnostic of XERARIONTA, SENSU STRICTO. Two undescribed species of XERARIONTA, SENSU STRICTO occur in the Brule Member of the White River Formation in the Douglas area, Wyoming (E. Evanoff & Roth, in preparation); the stratigraphically lowest occurrence is near a bed dated 33.9 Ma (early Oligocene).

Helminthoglypta bozemanensis Roth, 1986, from the Bozeman Group of western Montana, about 36 Ma in age (latest Eocene or earliest Oligocene), and *Helminthoglypta martini* (Hanna, 1920), from the John Day Formation of Oregon, with age bracketed loosely between 20 and 30 Ma (late Oligocene to early Miocene), show shell sculpture of collabral rugae cut into elongate granules, similar to that found in *Noyo intersessa* and some Recent species of *Helminthoglypta, sensu stricto* (Roth, 1986, 1988a).⁶ A species of *Helminthoglypta* probably assignable to *Coyote* occurs in Pliocene rocks of the Tehachapi Mountains, California (Roth & Hochberg, 1988). The origins of NOYO, *Helminthoglypta, sensu stricto* and XERARIONTA, SENSU STRICTO occur well out on their respective limbs of the consensus tree. The substantial radiation of the HELMINTHOGLYPTIDAE that underlies the framework of the tree must have taken place before the end of the Eocene.

Other fossils that have been assigned to HELMINTHOGLYPTIDAE probably are not referable to any modern genus of the clade. "*Helminthoglypta*" *alfi* Taylor, 1954, from the Barstow Formation (middle Miocene), southern California, has been assigned to *Coyote* (Reeder & Roth, 1988; Roth & Hochberg, 1988), but the description of its embryonic whorl sculpture (Taylor, 1954:76-77) does not accord well with any Recent taxon. *Greggelix? hochbergi* Roth & Megaw, 1989, from rocks of probable middle Eocene age in Chihuahua, Mexico (Roth & Megaw, 1989; Megaw, McDowell, & Roth, 1994), does not show any characters here regarded as diagnostic of terminal taxa; it could belong to SONORELLAMORPHA or HELMINTHOGLYPTAMORPHA. "*Helminthoglypta*" *obtusa* Anderson & Hanna, 1925, and "*Helminthoglypta?*" *stocki* G.D. Hanna, 1934, from the Eocene of southern California, are ca-

⁶ Assigning *H. bozemanensis* and *H. martini* to *Noyo* rather than to *Helminthoglypta* requires fewer assumptions about soft-part apomorphies not in evidence. The most conservative assignment is merely to HELMINTHOGLYPTAPHIM; cf. usage by Roth (1988b) of [Camaenidae] *stocki* and by Pierce (1992) of [Succineidae] *montana*. Including this type of sculpture as a character in the data set does not affect the relative positions of *Noyo intersessa* and *Helminthoglypta, sensu stricto* on the trees generated.

maenid land snails (Roth, 1988b). "*Micrarionta*" *dallasi* M. A. Hanna, 1927, from the Eocene of southern California, is a helicoid snail (Roth & Pearce, 1988). The referrals of *Glypterpes* and *Mesoglypterpes* to HELMINTHOGLYPTIDAE rest on tenuous readings of non-diagnostic shell characters.

By placing much of helminthoglyptid evolution in an early Tertiary time frame, this hypothesis obviates the need for scenarios of sudden or recent (e.g., post-Pleistocene) loss of reproductive structures. Of course, phylogenetic systematics does not rule out saltational speciation or any other evolutionary mechanism; at most it assumes only that evolution has occurred (Brooks & McLennan, 1991). Both *Helminthoglypta*, *sensu stricto* and XERARIONTA, SENSU STRICTO occur in settings of mesic paleoclimate (there is other climatic evidence, besides the presence of those genera, so this argument is not circular) and both have replete reproductive systems. Three of the instances of secondary simplification, *Mohavelix micrometalleus*, *Chamaearionta aquaealbae*, and *Eremariontoides argus*, are monotypic clades with their origins not constrained in time by any nodes farther up the tree. The phylogenetic hypothesis does not falsify a scenario of recent origins for these taxa, perhaps related to water conservation in an increasingly arid environment.

In contrast, the origins of SONORELLAMORPHA and the primary clades of HELMINTHOGLYPTAMORPHA must precede the origins of XERARIONTA, SENSU STRICTO and HELMINTHOGLYPTAPHIM in time. Even if the absence of accessory reproductive structures in SONORELLAMORPHA is apomorphic, it is not related to the late Tertiary onset of widespread aridity in the American Southwest (Axelrod, 1979). Pleistocene climatic fluctuations may be involved in the allopatric species diversity within SONORELLAMORPHA, but not in its origin as a clade.

From correspondence between the distribution of Bradybaenidae, Xanthonychidae, and Helminthoglyptidae and the tectonically accreted terranes around the Pacific rim, Miller & Naranjo-García (1991) drew the conclusion that those taxa had a common ancestry on a Mesozoic Gondwanan land mass ("Pacifica"; see Nur & Ben-Avraham, 1977; Jones et al., 1982) and were dispersed passively to the Americas on rafting fragments of continental crust. The present analysis impacts little on that model, except that, when fossil distribution is included, the range of HELMINTHOGLYPTIDAE is less congruent with accreted terranes than Miller & Naranjo-García (1991) assumed. (Schileyko [1991] reasserted the older alternative scenario of trans-Beringian dispersal, without offering any new reasons for preferring one story over the other.) The phylogenetic relations among the above taxa (and Epiphragmophoridae and Helicostylidae) are critical to the historical biogeography and still remain to be analyzed. Geographic components of taxon definitions, as noted above in the early concepts of Helminthoglyptidae, should be deleted when found, and future taxonomy be grounded in characters of the organisms themselves.

The rôle of heterochrony in bringing about the range of genital configurations should be investigated. For example, *Chamaearionta aquaealbae* may be neotenic with respect to CHAMAEARIONTALES in loss of (i.e., failure to develop) a verge and retention of periostracum and papillation into adulthood, and progenetic in its small size, low whorl number, and angular periphery. *Mohavelix micrometalleus* may be neotenic with respect to SONORELIX in failure to develop a spermathecal diverticulum, reduction of epiphallid caecum, and retention of periostracum and papillation into adulthood.

Here I remind myself that a hypothesis is a beginning, not an end in itself, and that my phylogenetic hypothesis is based on relatively few characters from only three systems. Future studies of the excretory, nervous, and alimentary systems will provide additional characters. The radula seems practically to have been written off for use in helminthoglyptid taxonomy, but should be reconsidered. Molecular data is potentially a rich field. Cladistic analysis should be extended to relations among species in speciose clades like SONORELLA and HELMINTHOGLYPTA, in which many new synapomorphies will have to be found if the trees are not to resemble the Ace comb I used to carry in my back pocket.

ACKNOWLEDGMENTS

For comments, discussion, helpful information, and/or tactical support I am grateful to David R. Lindberg, Emmett Evanoff, Michael Russell, and Elizabeth J. Kools. I thank Anatoly A. Schileyko for stimulating discussion and correspondence, and Diana Lipscomb for advice on method. Kenneth C. Emberton contributed information on polygyrid phylogeny and an anonymously signed review. Glenn R. Webb confirmed the characters of a slug genus described by him. Timothy A. Pearce commented on a draft of the introduction. Jacques Gauthier let me work with an unpublished manuscript by him and Kevin de Queiroz. Special thanks are reserved for Walter B. Miller for sometimes adversarial but ever warm collegiality in the study of helminthoglyptid snails, for discussing this study as it developed, for correcting my misinterpretation of *Noyo intersessa* anatomy, and for lending crucial specimens. This is Contribution No. 1581 from the Museum of Paleontology, University of California, Berkeley.

LITERATURE CITED

- ASHLOCK, P. D. 1971. Monophyly and associated terms. *Systematic Zoology* 20:63-69.
- AXELROD, D. I. 1979. Age and origin of Sonoran Desert vegetation. *Occasional Papers of the California Academy of Sciences* 132:1-74.
- AZUMA, M. 1982. *Colored Illustrations of the Land Snails of Japan*. Hoikusha Publishing Company, Ltd.: Osaka. xv + 333 pp.
- BAKER, H. B. 1943. Some Antillean helicids. *The Nautilus* 56: 81-91, pls. 9-11.

- BAKER, H. B. 1956. Family names in Pulmonata. *The Nautilus* 69:128-139.
- BAKER, H. B. 1959. Xanthonychidae (Pulmonata). *The Nautilus* 73:25-28.
- BALL, I. R. 1976. Nature and formulation of biogeographic hypotheses. *Systematic Zoology* 24:407-430.
- BEQUAERT, J. C. & W. B. MILLER. 1973. *The Mollusks of the Arid Southwest, with an Arizona Check List*. University of Arizona Press: Tucson. xvi + 271 pp.
- BERRY, S. S. 1943. On the generic relationships of certain Californian xerophile snails. *Transactions of the San Diego Society of Natural History* 10:1-24.
- BERRY, S. S. 1947. On the generic relationships of certain Lower Californian helicoid snails. *Leaflets in Malacology* 1:9-12.
- BERRY, S. S. 1959. Two Californian mountain snails of the genus *Helminthoglypta*—a problem in the relationship of species. *Transactions of the San Diego Society of Natural History* 11:329-344.
- BROOKS, D. R. & D. A. MCLENNAN. 1991. *Phylogeny, Ecology, and Behavior: a Research Program in Comparative Biology*. University of Chicago Press: Chicago. 434 pp.
- CARPENTER, J. M. 1988. Choosing among multiple equally parsimonious cladograms. *Cladistics* 4:291-296.
- CHRISTENSEN, C. C. & R. L. REEDER. 1981. New records of *Sonorella* (Pulmonata: Helminthoglyptidae) from the Table Top Mountains, Pinal County, Arizona, with a description of *Sonorella milleri*, new species. *The Southwestern Naturalist* 26:341-344.
- CHUNG, D. J. D. 1987. Courtship and dart shooting behavior of the land snail *Helix aspersa*. *The Veliger* 30:24-39.
- DE QUEIROZ, K. 1988. Systematics and the Darwinian Revolution. *Philosophy of Science* 55:238-259.
- DE QUEIROZ, K. & J. GAUTHIER. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Systematic Zoology* 39:307-322.
- DE QUEIROZ, K. & J. GAUTHIER. 1992. Phylogenetic taxonomy. *Annual Review of Ecology and Systematics* 23:449-480.
- DRAY, W. 1957. *Laws and Explanation in History*. Oxford University Press: Oxford.
- EBERHARD, W. G. 1985. *Sexual Selection and Animal Genitalia*. Harvard University Press: Cambridge, Massachusetts.
- EMBERTON, K. C. 1988. The genitalic, allozymic, and conchological evolution of the eastern North American Triodopsinae (Gastropoda: Pulmonata: Polygyridae). *Malacologia* 28:159-273.
- EMBERTON, K. C. 1991. Polygyrid relations: a phylogenetic analysis of 17 subfamilies of land snails (Mollusca: Gastropoda: Stylommatophora). *Zoological Journal of the Linnean Society* 103:207-224.
- EMBERTON, K. C. 1992. A translation of Hartmut Nordsieck's (1987) "Systematic revision of the Helicoidea (Gastropoda: Stylommatophora)". *Museum of Comparative Zoology Special Occasional Publication* 8:1-79.
- EVANOFF, E. & B. ROTH. 1992. The fossil land snail *Helix leidyi* Hall and Meek, 1855, a member of a new genus of Humboldtianidae (Gastropoda: Pulmonata). *The Veliger* 35:122-132.
- FAIRBANKS, H. L. & R. L. REEDER. 1980. Two new species of *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from the Pinaleno Mountains, Arizona. *Proceedings of the Biological Society of Washington* 93:395-404.
- FARRIS, J. S. 1969. A successive approximations approach to character weighting. *Systematic Zoology* 18:374-385.
- FARRIS, J. S. 1974. Formal definitions of parphyly and polyphyly. *Systematic Zoology* 23:548-554.
- FARRIS, J. S. 1976. Phylogenetic classification of fossils with Recent species. *Systematic Zoology* 25:271-282.
- FARRIS, J. S. 1988. HENNIG86, Version 1.5. Computer program distributed by author. Port Jefferson Station, New York.
- FARRIS, J. S. 1989. The retention index and the rescaled consistency index. *Cladistics* 5:417-419.
- GAUTHIER, J., R. ESTES & K. DE QUEIROZ. 1988. A phylogenetic analysis of Lepidosauriormorpha. Pp. 15-98 in R. Estes & G. K. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families*. Stanford University Press: Stanford, California.
- GREGG, W. O. 1948 [1949]. A new and unusual helicoid snail from Los Angeles County, California. *Bulletin of the Southern California Academy of Sciences* 47:100-102.
- GREGG, W. O. 1960. Derivation of the Helminthoglyptinae with particular reference to the desert forms. *American Malacological Union Bulletin* 26:45-46.
- GREGG, W. O. & W. B. MILLER. 1969. A new *Sonorella* from Phoenix, Arizona. *The Nautilus* 82:90-93.
- GREGG, W. O. & W. B. MILLER. 1974. Two new species of land snails from the Pinaleno Mountains, Arizona. *Bulletin of the Southern California Academy of Sciences* 73:146-151.
- GREGG, W. O. & W. B. MILLER. 1976. Two new species of *Helminthoglypta* (Mollusca: Pulmonata) from San Diego County, California. *Bulletin of the Southern California Academy of Sciences* 75:10-16.
- HENNIG, W. 1966. *Phylogenetic Systematics*. University of Illinois Press: Urbana. 263 pp.
- JONES, D. L., A. COX, P. CONEY & M. BECK. 1982. The growth of western North America. *Scientific American* 247:70-84.
- LEONARD, J. L. 1991. Sexual conflict and the mating systems of simultaneously hermaphroditic gastropods. *American Malacological Bulletin* 9:45-58.
- LEWIS, H. 1966. Speciation in flowering plants. *Science* 152:167-172.
- MEGAW, P. K. M., F. W. MCDOWELL & B. ROTH. Refinement of the age of certain Tertiary land mollusks (Gastropoda: Pulmonata): based on new U-Pb zircon ages from the Sierra Santa Eulalia, Chihuahua, Mexico. *Malacological Review* 27:109.
- MILLER, W. B. 1966. Three new *Sonorella* from southwest Arizona. *The Nautilus* 80:46-52, pls. 1, 2.
- MILLER, W. B. 1967a. Anatomical revision of the genus *Sonorella* (Pulmonata: Helminthoglyptidae). Ph.D. dissertation, Department of General Biology, University of Arizona, Tucson.
- MILLER, W. B. 1967b. Two new *Sonorella* from Rincon Mountains of Arizona. *The Nautilus* 81:54-61.
- MILLER, W. B. 1967c. Two new *Sonorella* from Sonora, Mexico. *The Nautilus* 80:114-119, 121-122.
- MILLER, W. B. 1967d. Two new *Sonorella* from Sonora, Mexico, with notes on southern limit of the genus. *The Nautilus* 81:1-6, 9.
- MILLER, W. B. 1968. New *Sonorella* from Arizona. *The Nautilus* 82:50-63.
- MILLER, W. B. 1969. A new *Sonorella* from the Salt River Mountains of Phoenix, Arizona. *The Nautilus* 82:87-89.
- MILLER, W. B. 1970. A new species of *Helminthoglypta* from the Mojave Desert. *The Veliger* 12:275-278.
- MILLER, W. B. 1971. The reproductive anatomy of *Tryonigens remondi* (Tryon, 1863): Helminthoglyptidae. *The Nautilus* 85:61-65.
- MILLER, W. B. 1972. *Greggelix*, a new genus of autochthonous land snails (Helminthoglyptidae) from Baja California. *The Nautilus* 85:128-135.

- MILLER, W. B. 1973. Saltational speciation in American Helminthoglyptidae. American Malacological Union Bulletin 1973:44.
- MILLER, W. B. 1976. New species of *Sonorella* (Pulmonata: Helminthoglyptidae) from New Mexico and Texas. The Nautilus 90:70-73.
- MILLER, W. B. 1981a. A new genus and a new species of helminthoglyptid land snail from the Mojave Desert of California. Proceedings of the Biological Society of Washington 94:437-444.
- MILLER, W. B. 1981b. A new *Greggelix* (Mollusca: Pulmonata: Helminthoglyptidae) from Baja California Sur, Mexico. Proceedings of the Biological Society of Washington 94:731-738.
- MILLER, W. B. 1981c. *Helminthoglypta reederi* spec. nov. (Gastropoda: Pulmonata: Helminthoglyptidae) from Baja California, Mexico. The Veliger 24:46-48.
- MILLER, W. B. 1982. A new subgenus and a new species of *Greggelix* (Gastropoda: Sigmurethra: Helminthoglyptidae) from the Sierra San Pedro Martir, Baja California, Mexico. The Veliger 24:345-348.
- MILLER, W. B. 1984. Three new species of *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from Arizona. Proceedings of the Biological Society of Washington 97:681-687.
- MILLER, W. B. 1985. A new subgenus of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae). The Veliger 28:94-98.
- MILLER, W. B. 1987. A new species of *Bunnya* (Gastropoda: Pulmonata: Humboldtianidae) from western Mexico, with notes on its life cycle and familial relationships. The Veliger 29:308-312.
- MILLER, W. B. & E. NARANJO-GARCÍA. 1991. Familial relationships and biogeography of the western American and Caribbean Helicoidea (Mollusca: Gastropoda: Pulmonata). American Malacological Bulletin 8:147-153.
- NARANJO-GARCÍA, E. 1988a. Four new *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from northwestern Sonora, Mexico. The Veliger 31:80-86.
- NARANJO-GARCÍA, E. 1988b. *Sonorella cananea*, a new species of land snail (Gastropoda: Pulmonata: Helminthoglyptidae) from Sonora, Mexico. The Southwestern Naturalist 22:81-84.
- NARANJO-GARCÍA, E. 1989. Four additional species of *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from Sonora, Mexico. The Veliger 32:84-90.
- NARANJO-GARCÍA, E. & W. B. MILLER. 1986. A new species of *Sonorella* (Gastropoda: Pulmonata: Helminthoglyptidae) from Sonora, Mexico. The Veliger 29:166-168.
- NELSON, G. 1979. Cladistic analysis and synthesis: principles and definitions, with a historical note on Adanson's Familles des Plantes (1763-1764). Systematic Zoology 28:1-21.
- NORDSIECK, H. 1987. Revision des Systems der Helicoidea (Gastropoda: Stylommatophora). Archiv für Molluskenkunde 118:9-50.
- NUR, A. & Z. BEN-AVRAHAM. 1977. Lost Pacific continent. Nature 279:41-43.
- O'HARA, R. J. 1988. Homage to Clio, or, toward an historical philosophy for evolutionary biology. Systematic Zoology 37: 142-155.
- O'HARA, R. J. 1992. Telling the tree: narrative representation and the study of evolutionary history. Biology and Philosophy 7:135-160.
- PEARCE, T. A. 1990. Phylogenetic relationships of *Micrarionta* (Gastropoda: Pulmonata) and distinctness of the species on San Nicolas Island, California. Malacological Review 23:1-37.
- PIERCE, H. G. 1992. The nonmarine mollusks of the late Oligocene-early Miocene Cabbage Patch fauna of western Montana. II. Terrestrial gastropod families other than Pupillidae (Pulmonata: Stylommatophora). Journal of Paleontology 66:610-620.
- PILSBRY, H. A. 1893-1895. Guide to the study of helices. Manual of Conchology, (2), 9:1-48, pls. 1-14 (1893); 49-160, pls. 15-40 (1894); 161-336, i-xlvi, pls. 41, 71, frontis. (1895).
- PILSBRY, H. A. 1907. On the soft anatomy of *E. (Micrarionta) hutsoni*. The Nautilus 20:138-139, pl. 9.
- PILSBRY, H. A. 1913. Notes upon some Lower Californian helices. Proceedings of the Academy of Natural Sciences of Philadelphia 65:380-393, pls. 15, 16.
- PILSBRY, H. A. 1918. On the generic position of *Sonorella wolcottiana* Bartsch. Proceedings of the Academy of Natural Sciences of Philadelphia 70:139-140.
- PILSBRY, H. A. 1927. Expedition to Guadalupe Island, Mexico, in 1922. Land and freshwater mollusks. Proceedings of the California Academy of Sciences, (4), 16:159-203, pls. 6-12.
- PILSBRY, H. A. 1939. Land Mollusca of North America (north of Mexico). Academy of Natural Sciences of Philadelphia, Monograph 3, 1(1):i-xvii, 1-573.
- PILSBRY, H. A. 1948. Land Mollusca of North America (north of Mexico). Academy of Natural Sciences of Philadelphia, Monograph 3, 2(2):i-xlvi, 521-1113.
- PILSBRY, H. A. & E. G. VANATTA. 1898. Anatomical notes on certain west American helices. Proceedings of the Academy of Natural Sciences of Philadelphia 50:67-71, pl. 1.
- REEDER, R. L. 1986. A new species of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) from the Cuyamaca Mountains of southern California. The Veliger 28: 444-447.
- REEDER, R. L. & W. B. MILLER. 1986a. A description of a new *Helminthoglypta* s.s. (Gastropoda: Pulmonata: Helminthoglyptidae) from San Diego County, California. The Veliger 29:129-131.
- REEDER, R. L. & W. B. MILLER. 1986a. A new species of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) from San Diego County, California. Proceedings of the Biological Society of Washington 99:137-139.
- REEDER, R. L. & W. B. MILLER. 1987. A new *Helminthoglypta* (*Rothelix*) (Gastropoda: Pulmonata: Helminthoglyptidae) from southern California with comments on its probable evolutionary relationships. The Southwestern Naturalist 32: 261-265.
- REEDER, R. L. & W. B. MILLER. 1988. A new *Helminthoglypta* (*Rothelix*) (Gastropoda: Pulmonata: Helminthoglyptidae) from Warner Springs, San Diego County, California. The Veliger 31:87-90.
- REEDER, R. L. & B. ROTH. 1988. A new subgenus of *Helminthoglypta* (Gastropoda: Pulmonata: Helminthoglyptidae) with the description of a new species from San Bernardino County, California. The Veliger 31:252-257.
- RICHARDSON, L. 1982. Helminthoglyptidae: catalog of species. Tryonia 6. 117 pp.
- ROTH, B. 1973. The systematic position of *Helminthoglypta traskii fieldi* Pilsbry, 1930 (Gastropoda: Stylommatophora). Bulletin of the Southern California Academy of Sciences 72: 148-155.
- ROTH, B. 1975. Description of a new terrestrial snail from San Nicolas Island, California (Gastropoda: Stylommatophora). Bulletin of the Southern California Academy of Sciences 74: 94-96.

- ROTH, B. 1981. Distribution, reproductive anatomy, and variation of *Monadenia troglodytes* Hanna and Smith (Gastropoda: Pulmonata) with the proposal of a new subgenus. Proceedings of the California Academy of Sciences 42:379-407.
- ROTH, B. 1982. The identity of "*Helminthoglypta*" *tularica* (Bartsch) (Gastropoda: Pulmonata). Bulletin of the Southern California Academy of Sciences 81:101-105.
- ROTH, B. 1984. *Lysinoe* (Gastropoda: Pulmonata) and other land snails from Eocene-Oligocene of Trans-Pecos Texas, and their paleoclimatic significance. The Veliger 27:200-218.
- ROTH, B. 1986. Land mollusks (Gastropoda: Pulmonata) from early Tertiary Bozeman Group, Montana. Proceedings of the California Academy of Sciences 44:237-267.
- ROTH, B. 1987a. A new and polytypic species of *Helminthoglypta* (Gastropoda: Pulmonata) from the Transverse Ranges, California. The Veliger 30:184-189.
- ROTH, B. 1987b. A new species of *Helminthoglypta* (Gastropoda: Pulmonata) from the North Coast Ranges of California, with observations on the spermatophore. Wasmann Journal of Biology 44:57-65.
- ROTH, B. 1988a. A new Recent species of *Helminthoglypta* (Gastropoda: Pulmonata) from the Klamath Mountains, California, and redescription of an Oligo-Miocene species from Oregon. Wasmann Journal of Biology 45:16-25.
- ROTH, B. 1988b. Camaenid land snails (Gastropoda: Pulmonata) from the Eocene of southern California and their bearing on the history of the American Camaenidae. Transactions of the San Diego Society of Natural History 21:203-220.
- ROTH, B. & F. G. HOCHBERG, JR. 1988. A new species of *Helminthoglypta* (*Coyote*) (Gastropoda: Pulmonata) from the Tehachapi Mountains, California. The Veliger 31:258-261.
- ROTH, B. & F. G. HOCHBERG, JR. 1992. Two new species of *Helminthoglypta* (Gastropoda: Pulmonata) from southern California, with comments on the subgenus *Charodotes* Pilsbry. The Veliger 35:338-346.
- ROTH, B. & P. K. M. MEGAW. 1989. Early Tertiary land mollusks (Gastropoda: Pulmonata) from Sierra Santa Eulalia, Chihuahua, Mexico, and the origins of the North American arid-land mollusk fauna. Malacological Review 22:1-16.
- ROTH, B. & T. A. PEARCE. 1988. "*Micrarionta*" *dallasi*, a helicoid (prosobranch), not a helminthoglyptid (pulmonate) land snail: paleoclimatic implications. The Southwestern Naturalist 33:117-119.
- ROWE, T. 1987. Definition and diagnosis in the phylogenetic system. Systematic Zoology 36:208-211.
- SCHILEYKO, A. A. 1978. Land mollusks of the superfamily Helicoidea. Fauna of the U.S.S.R., Mollusks, 3(6):1-384.
- SCHILEYKO, A. A. 1979. The system of the order Geophila (=Helicida) (Gastropoda Pulmonata). Pp. 44-69 in O. A. Scarlato (ed.), Morphology, Systematics and Phylogeny of Mollusca. Proceedings of the Zoological Institute, Academy of Sciences of the U.S.S.R. 80.
- SCHILEYKO, A. A. 1991. Taxonomic status, phylogenetic relations and system of the Helicoidea sensu lato (Pulmonata). Archiv für Molluskenkunde 120:187-236.
- SIMPSON, G. G. 1961. Principles of Animal Taxonomy. Columbia University Press: New York.
- SMITH, A. G., W. B. MILLER, C. C. CHRISTENSEN & B. ROTH. 1990. Land Mollusca of Baja California, Mexico. Proceedings of the California Academy of Sciences 47:95-158.
- SOKAL, R. R. & F. J. ROHLF. 1981. Taxonomic congruence in the Leptopodomorpha re-examined. Systematic Zoology 30:309-325.
- SOLEM, A. 1984. A world model of land snail diversity and abundance. Pp. 6-22 in A. Solem and A. C. van Bruggen (eds.), World-Wide Snails: Biogeographical Studies on Non-Marine Mollusca. E. J. Brill/Dr. W. Backhuys: Leiden.
- SOLEM, A. 1991. The next challenge: life styles and evolution. American Malacological Bulletin 8:173-175.
- SOLEM, A. & C. C. CHRISTENSEN. 1984. Camaenid land snail reproductive cycle and growth patterns in semiarid areas of north-western Australia. Australian Journal of Zoology 32:471-491.
- TAYLOR, D. W. 1954. Nonmarine mollusks from Barstow Formation of southern California. U. S. Geological Survey Professional Paper 254-C:67-80, pl. 20.
- WATROUS, L. E. & Q. D. WHEELER. 1981. The out-group comparison method of character analysis. Systematic Zoology 30:1-11.
- WEBB, G. R. 1942. Comparative observations of the mating habits of three California landsnails. Bulletin of the Southern California Academy of Sciences 41:102-108.
- WEBB, G. R. 1951. An instance of amixia between two species of landsnails (Pulmonata, Helminthoglyptidae). American Naturalist 85:137-139.
- WEBB, G. R. 1952a. Pulmonata, Helminthoglyptidae: sexological data on the land snails, *Cepolis maynardi* & *Helminthoglypta traski fieldi* and their evolutionary significance. Gastropodia 1:4-5.
- WEBB, G. R. 1952b. Pulmonata, Xanthonychidae: comparative sexological studies of the North American land-snail, *Monadenia fidelis* (Gray)—a seeming ally of Mexican helicoids. Gastropodia 1:1-3.
- WEBB, G. R. 1959. Two new north-western slugs, *Udosarx lyrata*, and *Gliabates oregonia*. Gastropodia 1:22-23.
- WEBB, G. R. 1961. The phylogeny of American land snails with emphasis on the Polygyridae, Arionidae, and Ammonitellidae. Gastropodia 1:31-44.
- WEBB, G. R. 1990. Notes on the sexology of *Sonorella simmonsii* Miller. Gastropodia 2:22-24.
- WILEY, E. O. 1979. An annotated Linnean hierarchy, with comments on natural taxa and competing systems. Systematic Zoology 28:308-337.
- WILEY, E. O. 1981. Phylogenetics: the Theory and Practice of Phylogenetic Systematics. John Wiley and Sons: New York.
- WILEY, E. O. 1989. Kinds, individuals, and theories. Pp. 289-300 in M. Ruse (ed.), What the Philosophy of Biology Is. Kluwer Academic Publishers: Dordrecht.
- ZILCH, A. 1959-1960. Gastropoda, Teil 2. Euthyneura. Handbuch der Paläozoologie, 6(2):1-400 (1959), 401-834 (1960).

APPENDIX: NEW TAXA AND PHYLOGENETIC DEFINITIONS OF NAMED TAXA

New Taxa of the Genus Group

CAHUILLUS, new genus. Type species: *Sonorella wolcottiana* Bartsch, 1903. Definition: CAHUILLUS consists of *Cahuillus indioensis wolcottianus* (Bartsch, 1903) and all other taxa that share a more recent common ancestor with it than with EREMARIONTA. Diagnostic character states: double-walled section of epiphallus cylindrical, less than 0.4 times as long as penis, extending into verge (9C). Additional referred taxa: *Cahuillus indioensis indioensis* (Yates, 1890), *Cahuillus indioensis cathedralis* (Willett, 1930), *Cahuillus greggi* (Miller, 1981), *Cahuillus mexicanus* (Pilsbry & Lowe, 1934). Many nom-

inal species and subspecies conventionally referred to *Eremarionta* have not yet been dissected; some may prove to belong to CAHUILLUS. The conventional subspecific relationship of *C. i. indioensis*, *C. i. wolcottianus*, and *C. i. cathedralis* is retained pending further study of the group. *Cahuillus mexicanus* formerly was regarded as a subspecies of *Eremarionta rowelli*, but its anatomy is that of CAHUILLUS. Etymology: named for prehistoric Lake Cahuilla, which formerly occupied much of the Salton Trough in southern California.

MARICOPELLA, new genus. Type species: *Sonorella allynsmithi* Gregg & Miller, 1969. Definition: MARICOPELLA consists of *Maricopella allynsmithi* (Gregg & Miller, 1969) and all other species that share a more recent common ancestor with it than with SONORELLALES. Diagnostic character states: minute verge (12B); thick penial sheath enveloping whole penis (13B). Etymology: named for Maricopa County, Arizona.

NICOLENEA, new subgenus. Type species: *Micrarionta opuntia* Roth, 1975. Definition: NICOLENEA consists of *Micrarionta (Nicolenea) opuntia* Roth, 1975, and all other species that share a more recent common ancestor with it than with MICRARIONTA, SENSU STRICTO. Diagnostic character states: descending mucus gland absent (2C); dart sac absent (5C); papillation extensive over shell, including body whorl (18C). Tight coiling of the body whorl (19A) and absence of spermathecal diverticulum (6A) are synapomorphies shared with MICRARIONTA, SENSU STRICTO. Additional referred taxa: *Micrarionta sodalis* (Hemphill, 1901), *Micrarionta micromphala* Pilsbry, 1939, *Micrarionta opuntia*, *M. sodalis*, and *M. micromphala* form a clade diagnosed by the synapomorphies of translation rate slope > 0.05 (more domed spire), upper lip not reflected or recurved, and aperture wider than high (Pearce, 1990). Although *M. micromphala* and *M. sodalis* are extinct and their anatomy unknown, I refer them to NICOLENEA on the basis of these shell characters. Etymology: named for San Nicolas Island, California.

NOYO, new genus. Type species: *Helminthoglypta intersessa* Roth, 1987. Definition: NOYO consists of *Noyo intersessa* (Roth, 1987) and all other species that share a more recent common ancestor with it than with HELMINTHOGLYPTANIKI. Diagnostic character states: malleation (17A) and granular sculpture formed by collateral rugae cut by striae nearly parallel to suture; y-shaped, heavily muscularized common duct of mucus glands. Roth's (1987b) observations of an atrial sac in *N. intersessa* were incorrect; the dart sac inserts directly on the vagina. Malleated and granular sculpture occur as homoplasies in *Helminthoglypta*, sensu stricto, which has an atrial sac with vagina inserting at its base (1C). Additional referred taxa: the fossil *Helminthoglypta bozemanensis* Roth, 1986, and *H. martini* (Hanna, 1920) may be species of NOYO. Etymology: named for the Noyo River, a major stream in the region of *N. intersessa*; gender feminine.

New Suprageneric Taxa

CHAMAEARIONTALES, new taxon, consists of *Chamaearionta aquaealbae* and all taxa that share a more recent common ancestor with it than with HELMINTHOGLYPTALES.

EREMARIONTAPHIM, new taxon, consists of *Eremarionta rowelli desertorum* and all taxa that share a more recent common ancestor with it than with HELMINTHOGLYPTAPHIM.

HELMINTHOGLYPTAINA, new taxon, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with SONORELIX.

HELMINTHOGLYPTALES, new taxon, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with CHAMAEARIONTALES.

HELMINTHOGLYPTAMORPHA, new taxon, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with SONORELLAMORPHA.

HELMINTHOGLYPTANIKI, new taxon, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with *Noyo intersessa*.

HELMINTHOGLYPTAPHIM, new taxon, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with EREMARIONTAPHIM.

HELMINTHOGLYPTOTES, new taxon, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with MICRARIONTA.

SONORELLALES, new taxon, consists of *Sonorella hachitana* and all taxa that share a more recent common ancestor with it than with *Maricopella allynsmithi*.

SONORELLAMORPHA, new taxon, consists of *Sonorella hachitana* and all taxa that share a more recent common ancestor with it than with HELMINTHOGLYPTAMORPHA.

XERARIONTALES, new taxon, consists of *Xerarionta levis canescens* and all taxa that share a more recent common ancestor with it than with HELMINTHOGLYPTALES.

Phylogeny-Based Definitions of Existing Taxa

EREMARIONTA Pilsbry, 1913, consists of *Eremarionta rowelli desertorum* and all taxa that share a more recent common ancestor with it than with CAHUILLUS.

EREMARIONTA, SENSU STRICTO consists of *Eremarionta rowelli desertorum* and all taxa that share a more recent common ancestor with it than with *Eremariontoides argus*.

GREGGELIX Miller, 1972, consists of *Greggelix indigena* and all taxa that share a more recent common ancestor with it than with XERARIONTA.

HELMINTHOGLYPTA Ancey, 1887, consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with ROTHELIX.

HELMINTHOGLYPTIDAE consists of *Helminthoglypta tudiculata* and all taxa that share a more recent common ancestor with it than with the clade (Xanthonychidae, Bradybaenidae).

- HERPETEROS Berry, 1947, consists of *Herpeteros inglesiana* and all taxa that share a more recent common ancestor with it than with *Chamaearionta aquaealbae*.
- MARTIRELIX Miller, 1982, consists of *Martirelix babrakzaii* and all taxa that share a more recent common ancestor with it than with "*Greggelix, sensu stricto*".
- MICRARIONTA Ancy, 1880, consists of *Micrarionta facta* and all taxa that share a more recent common ancestor with it than with HELMINTHOGLYPTOTES.
- MICRARIONTA, SENSU STRICTO consists of *Micrarionta facta* and all taxa that share a more recent common ancestor with it than with NICOLENEA.
- MYOTOPHALLUS Pilsbry, 1939, consists of *Myotophallus rooseveltiana fragilis* and all taxa that share a more recent common ancestor with it than with SONORELLA.
- ROTHELIX Miller, 1985, consists of *Rothelix lowei* and all taxa that share a more recent common ancestor with it than with HELMINTHOGLYPTA.
- SONORANAX Pilsbry, 1939, consists of *Sonoranax dalli* and all taxa that share a more recent common ancestor with it than with "*Sonorella, sensu stricto*".
- SONORELIX Berry, 1943, consists of *Sonorelix borregoensis* and all taxa that share a more recent common ancestor with it than with HELMINTHOGLYPTAINA.
- SONORELIX, SENSU STRICTO consists of *Sonorelix borregoensis* and all taxa that share a more recent common ancestor with it than with *Mohavelix micrometalleus*.
- SONORELLA Pilsbry, 1900, consists of *Sonorella hachitana* and all taxa that share a more recent common ancestor with it than with MYOTOPHALLUS.
- XERARIONTA Pilsbry, 1913, consists of *Xerarionta levis canescens* and all taxa that share a more recent common ancestor with it than with GREGGELIX.
- XERARIONTA, SENSU STRICTO consists of *Xerarionta levis canescens* and all taxa that share a more recent common ancestor with it than with "*Plesarionta*".